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A STUDY OF SOME ECOLOGIC FACTORS AFFECTING THE DISTRIBUTION OF PROTOZOA

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A STUDY OF SOME ECOLOGIC FACTORS AFFECTING THE DISTRIBUTION OF PROTOZOA

INTRODUCTION

Many of the lower organisms appear to have a truly cosmopolitan distribution; among such the protozoa are pre-eminent, whether they be soil dwellers or inhabitants of sea or fresh water. Indeed, many species have been recorded from both marine and fresh water habitats and it is a puzzle how they can so readily adjust themselves to such extremes of osmotic pressure, pH, and chemical environment as to dwell in each of the two situations. Finley (1930) has recently investigated the tolerance of 36 species of protozoa for as wide a range of environmental change as transferring them from their fresh water habitat to sea water. Four species stood a direct transfer, while 17 others adapted themselves to the new environment if the transfer was effected gradually, but ten per cent sea water was fatal to 11 species, while the remainder were tolerant of varying concentrations of less than 100 per cent. Yocom (1934) repeated this work on *Euplotes charon* and *E. patella* obtaining results contradictory to those of Finley.

I have transferred *Cyclidium glaucoma* directly to sea water, confirming the results of Finley with this organism. As Noland (1925) has pointed out, in the protozoa we are usually dealing with single cells set apart from their environment by nothing more than a thin pellicle and plasma membrane. Possibly the ready permeability and thinness of the protoplasmic body enable them to make quick adjustments. It is to be expected then that many protozoan species will exhibit a wide tolerance for environmental variations in light, temperature, hydrogen ion concentration, percentage of various salts, percentage of dissolved oxygen, the presence of various organic compounds, food substances, presence of other species and the like. Such a tolerance is indeed familiar to the more than casual student of these organisms, who notes that whenever and wherever he takes a sample of stagnant water for examination, certain species will almost invariably appear, while if he inoculates some of this material into laboratory cultures of the several infusions of hay, wheat, peptone or other media commonly used, there is a fairly definite succession of protozoan species, until the infusions finally approach a static condition wherein only an occasional active protozoon may be observed. These sequences and conditions have been recorded by Woodruff (1912), Fine (1925), and others. Nevertheless the list of commonly occurring species is sooner or later exhausted whether in a laboratory culture or field environment, and such additional forms as are thereafter found are thought of as "rare," i.e., restricted as to environment.

This cosmopolitan distribution applies to some of the rarely occurring species as well as the common ones. It is well illustrated by *Menoidium*

gracile, a large and sharply differentiated species which I found five times in the Muscle Shoals area and regarded as a new species until I was able to consult a paper by Playfair (1921) and found he had recorded it from Australia. Any search for factors governing the presence or absence of a given protozoan species in a given habitat at a given time, is difficult at best, but it is hoped that the accumulated data herein presented and discussed may be a contribution.

MATERIAL AND METHODS

In the past ten years I have examined several hundred plankton samples taken from a variety of habitats for the purpose of enumerating their protozoan fauna. Part of this work was done at the Oceanographic Institution at Woods Hole, Mass.; some in New Jersey; some in the Muscle Shoals area of Tennessee, Alabama and Mississippi; some at Reelfoot Lake in Tennessee; and some at Cincinnati, Ohio.

These habitats are shown in Table 1. Column 1 includes a wide variety of situations but all the others include more restricted environments. Imhoff tanks are digestion chambers, characteristically anaerobic and dark, receiving and digesting raw sewage; trickling filters and activated sludge chambers are likewise parts of sewage disposal plants, but well aerated.

The samples referred to herein were well mixed where taken and were examined soon after taking; if a long trip to the laboratory was necessary an iced container was used. In a few cases field examination of settled samples was made, but in most cases the water samples were centrifuged in 50 cc. tubes and the catch examined. All were fresh samples, no preserved ones having been studied.

Of course, not all the species in the samples were enumerated, nor were all those seen familiar to me. But only the most thoroughly examined samples are treated here, and the great majority of forms were either known to me, or were identified; probably only an occasional species was not observed.

THE NATURAL DISTRIBUTION OF PROTOZOAN SPECIES

Table 1 gives a list of protozoa occurring in eight general habitat types. Only those marine forms are included which are morphologically indistinguishable from fresh water species; for a more complete list of marine forms my paper (1936) on the Woods Hole protozoa should be consulted. This table does not consider either seasonal or light factors; except for the marine forms the samples were taken at various times of the year; all samples were taken in daylight.

A study of Table 1 will show that despite the widespread distribution of any protozoan species, there is probably a small chance of finding any given species in a chance habitat. A species may at times occupy a certain habitat in enormous numbers, as was the case with "*Spirostomum* Pond" at Woods Hole, or the familiar bloom of *Euglena sanguinea* on hot shallow ponds in the later summer, but such dominance is usually highly exclusive of other species and may be short lived. There are few protozoa which

might confidently be expected to occur in a random sample. In Column 1 only three species occurred in 50 per cent or more of the samples examined; viz., *Cyclidium glaucoma*, *Cinetochilum margaritaceum* and *Trachelomonas volvocina*. For these three organisms we may safely assume a tolerance of wide environmental changes, for they are inevitable in the habitats under consideration.

Perhaps the most evident fact shown by Table 1 is that some protozoa tolerate an enormous variation in environment. The habitats studied may be loosely divided into clean and polluted ones. Actually there are perhaps as many habitats represented as there are samples included by the table and only a few protozoa occupy most of the habitats sampled. Eighteen species occur in the four "clean water" situations, fourteen in all situations. Only four ciliates, *Chilodonella cucullulus*, *Colpidium colpoda*, *Cinetochilum margaritaceum* and *Cyclidium glaucoma* were found in such extremes as clean ponds, the ocean and the anaerobic darkness of an Imhoff tank; these same four successfully endured activated sludge to which sucrose had been added to a concentration of 12,000 p.p.m.

In one respect the table is misleading. Ninety-four species have been recorded from only one type of habitat, most of these appearing only in Column 1, and yet they are not necessarily rare. The testate rhizopods, for example *Nebela collaris*, are common in sphagnum bogs, not one of which was sampled in this study. Some species are common enough where they occur, as *Spirozoa caudatum* which was an abundant ciliate during several months in the small Reservation Pool referred to below, but which I have encountered only once elsewhere. Other species are definitely rare; I have seen *Trachelius ovum* only once in my lifetime, yet it is a fairly large and unmistakable ciliate.

Certain protozoa may be looked for in certain types of loci, but be rare or lacking in others. Hausman (1917) listed some of these groups, recognizing environmental types of habitat by physical characteristics. If it were possible to break down the sampling stations of Column 1 to smaller groups we might gain an idea as to what sort of pool would probably yield certain species as *Rhipidodendron splendidum* or *Ophrydium versatile* or *Clathrulina elegans*, but we would be no nearer a determination of the factors responsible for its existence in such a situation. To get *Trimyema compressa* for study it is only necessary to pour raw domestic sewage into a tube sufficiently long so that anaerobic decomposition takes place at the bottom, and in a few days this ciliate will appear in the bottom sludge. These illustrations show that in a general way we correlate definite habitat types with particular protozoa or groups of protozoa but fail to recognize the specific factors favorable or restrictive to those places. It is evidently our lack of knowledge of these specific determinative factors that makes our correlations general, for despite the environmental variations shown to be tolerated in Table 1, only about 6 per cent of the species in Column 1 could be reason-

TABLE 1. THE LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS;
SHOWING THE NUMBER OF TIMES EACH SPECIES OCCURRED IN THE
TOTAL NUMBER OF SAMPLES EXAMINED

Species Present	Frequency of Occurrence							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
Total Number of Samples Examined	70	20	25	40	40	50	50	40
<i>Sarcodina</i>								
1. Acanthocystis aculeata	13	5	3
2. Actinophrys sp.	7	1	..	3
3. " sol.	16	2	1	2	1	..
4. Actinosphaerium eichorni	8	1
5. Allogromia fluviatilis	6	1
6. Amoeba proteus	25	1	1	..	16	3
7. " radiosa	16	1	2	..	1	1	7	1
8. " striata	1	1	3	23	1
9. " tachypodia	14	1	..	16	9
10. " verrucosa	11	1	1	23	3
11. Arcella dentata	8	1
12. " discoides	6	2	..
13. " mitrata	..	1
14. " vulgaris	24	2	3	..	4	1	40	26
15. Astrodiscus radians	2
16. Centropyxis aculeata	8	..	1	27	16
17. Chlamydomorphys stercorea	1	3	18	5
18. " minor	2	6	6	2
19. Clathrulina elegans	2	1
20. Cyphoderia ampulla	1
21. Cochliopodium bilimbosum	3	7	22	12
22. Diffugia acuminata	2	..
23. " corona	2	3	..
24. " globosa	1
25. " lebes	..	5	1	2	..
26. " pyriformis	12	2	1	14	..
27. " urceolata	1
28. Euglypha alveolata	8	..	2	..	2	12	12	5
29. " ciliata	3
30. Hartmanella hyalina†	17	1	2	3	23	22	35	30
31. Heterophrys myriapoda	3	1	..
32. Hyalodiscus rubicundus	2	1	1	..
33. Lecquereusia modesta	1
34. Microchlamys patella	1
35. Nebela collaris	1
36. Nuclearia simplex	7	1	1	3	18	23
37. Paulinella chromatophora	2
38. Pamphagus mutabilis	3	3	..
39. Pelomyxa palustris	6
40. Pinacocystis fluviatilis	1	1
41. Pseudodiffugia gracilis	2	1	1	..
42. Quadrula symmetrica	1
43. Raphidiophrys elegans	5	2	..
44. " pallidum	2	1
45. Trinema lineare	11	1	1	2	11	2
46. Vahlkampfia albida	26	..	3	..	2	4	18	7
47. " guttula	17	11	13	27	10
48. " limax	20	2	8	11	22	17
49. Vampyrella lateritia	5	1

(†) Includes Dimastigamoeba gruberii; the two could not be distinguished in the trophic state.

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS
(Continued)

Species Present	Frequency of Occurrence							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
<i>Mastigophora</i>								
50. <i>Actinactis mirabilis</i>	2
51. <i>Anisonema ovale</i>	19	1	1	7	..	1	1	6
52. " <i>emarginatum</i>	2	2	..
53. " <i>truncatum</i>	2	4	..
54. <i>Anthophysa vegetans</i>	6	2	20	11	6	..
55. <i>Ascoglena vaginicola</i>	1
56. <i>Astasia dangeardi</i>	8	..	1	2	..
57. " <i>inflata</i>	3	1	..
58. " <i>klebsii</i>	2	..	1
59. " <i>ocellata</i>	3
60. <i>Bicoeca lacustris</i>	1	1
61. <i>Bodo angustus</i>	4	1	2	1	8	8	..	1
62. " <i>agilis</i>	1	2
63. " <i>caudatus</i>	1	3	5	20	8	2
64. " <i>sp.</i>	21	4	1
65. " <i>globosus</i>	8	2	3	9	5	2	4	1
66. " <i>lens</i>	16	5	1	2	2	3	..	1
67. " <i>minimus</i>	2	..	1	..	1	1
68. " <i>mutabilis</i>	2	5	9
69. " <i>ovatus</i>	1	2	12	17	6	2
70. <i>Bodopsis godboldi</i>	1	1	..	2
71. <i>Carteria</i> spp.....	2	1	1
72. <i>Ceratium hirundinella</i>	1
73. <i>Cercobodo crassicauda</i>	3	..	1	2	5	8	3	1
74. " <i>caudatus</i>	1	..	9	18	4	2
75. " <i>longicauda</i>	2	3	6	17	9	3
76. " <i>ovatus</i>	3
77. <i>Cercomonas</i> sp.....	2
78. " <i>sp.</i>	13	11	..	2
79. <i>Chilomonas oblonga</i>	5
80. " <i>paramecium</i>	9	2	5	2	2	2	9	2
81. <i>Chlamydomonas</i> spp.....	48	16	6	3	16	15	2	..
82. <i>Chlorogonium elongatum</i>	2	1
83. " <i>euchlora</i>	3	..	1	1	1
84. <i>Chroomonas cyaneus</i>	2	3	1	..	2
85. " <i>nordstetii</i>	2	1
86. " <i>pulex</i>	9	3	..	1
87. " <i>setoniensis</i>	11	3	2
88. <i>Chromulina ovalis</i>	19	3
89. " <i>sp.</i>	2	3	..	1
90. <i>Chrysamoeba radians</i>	1
91. <i>Chrysopsis sagene</i>	1
92. <i>Chrysocapsa plankton</i>	1
93. <i>Clautriavia parva</i>	6	16
94. <i>Codonocladium solitaria</i>	1
95. <i>Codonosiga botrytis</i>	3
96. <i>Collodictyon triciliatum</i>	7	3	..	1	1	..	3	..
97. <i>Cryptochrysis commutata</i>	3	2
98. <i>Cryptoglena pigra</i>	2	3	1
99. <i>Cryptomonas erosa</i>	28	11	4	1	3
100. " <i>ovata</i>	27	11	2	..	6
101. <i>Cyathomonas truncata</i>	29	1	..	1	..	1	3	2

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(Continued)

Species Present	Frequency of Occurrence							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
102. Dinobryon acuminata	1
103. " euryostomum	4	2
104. " sertularia	7	1	2
105. Dinomonas vorax	2	3	6	..	2
106. Distigma proteus	8	..	5	..	1	3	1	1
107. Entosiphon sulcatum	22	2	7	16	9
108. " ovatum	1	..	1
109. Eudorina elegans	6	8	3
110. Euglena acus	5	1	1
111. " acutissima	6	1	3
112. " deses	10	6	3
113. " ehrenbergii	5
114. " gracilis	15	1	3	1	1
115. " intermedia	3
116. " limnophila	1
117. " mutabilis	7	2	1	1
118. " pisciformis	28	5	2	..	4
119. " polymorpha	28	3	2	..	5	5
120. " proxima	1
121. " quartana	1	..	9	2	3	3
122. " sanguinea	12	2
123. " spirogyra	13	1
124. " sociabilis	17	7
125. " spiroides	1
126. " terricola	1
127. " torta	2
128. " tripteris	3	..	1	..	2
129. " viridis	30	3	1	..	11	1	1	..
130. Gonium pectorale	16	7	4
131. " sociale	1	1
132. Gonyostomum semen	7	2
133. Gymnodinium cyaneus	2
134. " palustre	8	1
135. Heteronema acus	4	1	2	1	..
136. " globuliferum	1
137. Hexamitus crassus	1	..	6	..	9	6	4	4
138. " inflatus	12	16	3	2
139. Hyalogonium klebsii	3
140. Kephyrion ovum	..	3	2
141. Lepocinclis ovum	12	2	4
142. " texta	1	1
143. Lobomonas rostrata	2	1	1
144. Mallomonas spp.	23	9	7
145. Mastigamoeba longifilum	1	4	13	18	3	1
146. " reptans	5	..	2	..	8	16	1	..
147. Mastigella simplex	1	2	9
148. Mastigina setosa	1
149. Menoidium faicatum	1
150. " gracile	5
151. " sp.	6
152. " incurvum	6	..	11	..	1	2	3	2
153. " tortuosum	1	..	1
154. Monas amoebina	7	1	..	2	6	2	12	10
155. " minima	1	22	13	31	28

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	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Tricklingfilter	Activated sludge chamber
156. <i>Monas obliqua</i>	3	11	3	11	12
157. " <i>vivipara</i>	4	2	2	4	1	2	8	5
158. " <i>vulgaris</i>	11	4	6	2	3	2
159. <i>Monosiga ovata</i>	2	1	1	..
160. " <i>robusta</i>	3
161. <i>Multicilia lacustris</i>	1	3
162. <i>Notosolenus orbicularis</i>	21	2	2	5	2	23	12	9
163. <i>Ochromonas variabilis</i>	1	..	1	1
164. <i>Oicomonas ocellata</i>	1	3
165. " <i>obliqua</i>	1
166. " <i>termo</i>	7	2	..	3	23	5	17	11
167. " <i>socialis</i>	3	1	..	2	11	21	7	20
168. " <i>steinii</i>	8	2	1	1
169. <i>Pandorina morum</i>	11	15	3
170. <i>Peranema ovalis</i>	8	..	1
171. " <i>trichophorum</i>	25	1	1	2	5	4	30	31
172. <i>Petalomonas carinata</i>	10	3	2
173. " <i>mediocanellata</i>	2	2
174. " <i>steinii</i>	1	..	1
175. <i>Phacotus lenticularis</i>	2
176. <i>Phacus hispidula</i>	1
177. " <i>longicauda</i>	12	..	3
178. " <i>lunularis</i>	2
179. " <i>orbicularis</i>	3
180. " <i>pleuronectes</i>	5
181. " <i>pyrum</i>	11	..	1
182. " <i>sp.</i>	1
183. " <i>stokesii</i>	3	..	2	..	1
184. " <i>torta</i>	1
185. " <i>triqueter</i>	15	2	4
186. <i>Platytheca micropora</i>	2	1
187. <i>Pleodorina californica</i>	1
188. <i>Pleuromonas jaculans</i>	7	1	1	3	18	29	26	21
189. <i>Polytoma uvella</i>	2	..	13	8	3	1
190. <i>Protochrysis viridis</i>	1	1
191. <i>Rhipidodendron splendidum</i>	3
192. <i>Rynchomonas nasuta</i>	1	1	7	9	8	9
193. <i>Salpingoeca marsoni</i>	1
194. <i>Sphaerella lacustris</i>	2
195. <i>Sphaerellopsis fluviatile</i>	1
196. <i>Spondylomorum quaternarium</i>	1
197. <i>Synura uvella</i>	17	2	6	..	1	..
198. <i>Tetramitus decissus</i>	1	15	15	2	..
199. " <i>pyriformis</i>	1	..	3	..	20	10	5	1
200. <i>Thoracomonas phacotoides</i>	4	4
201. <i>Trachelomonas acanthostoma</i>	1
202. " <i>armata</i>	7	1
203. " <i>bernardi</i>	1
204. " <i>conspersa</i>	2	1
205. " <i>crebea</i>	1
206. " <i>euchlora</i>	12	1	1	1
207. " <i>fluviatilis</i>	1
208. " <i>globularis</i>	5

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(Continued)

Species Present			Frequency of Occurrence							
			Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
209.	Trachelomonas	hispida	24	6	6
210.	"	horrida	1
211.	"	intermedia	1
212.	"	sp.	10	6
213.	"	sp.	3
214.	"	oblonga	4
215.	"	obovata	1
216.	"	orbicularis	1
217.	"	raciborskii	1	3
218.	"	reticulata	1
219.	"	rugosa	1
220.	"	rugulosa	1
221.	"	spiculifera	1
222.	"	triangularis	..	1
223.	"	teres	3
224.	"	urceolata	1	1
225.	"	verrucosa	4	2	1
226.	"	vermicularis	..	1
227.	"	vestita	1	1
228.	"	vulvocina	43	8	8	..	7
229.	Trepomonas	agilis	2	..	1	4	17	31	3	1
230.	"	rotans	2	..	22	10	2	2
231.	Trigonomonas	compressa	1	..	2	..	3
232.	Tropidoscyphus	octacostatus	1	3
233.	Urceolus	sabulosus	3	1
<i>Infusoria</i>										
234.	Amphisia	(kessleri?)	4	1
235.	Aspidisca	costata	18	..	1	5	3	3	31	29
236.	"	lynceus	7	6	5
237.	"	turrita	2	1	1
238.	Balanitozoon	agile	5	..	1	..	1
239.	Balanonema	biceps	1
240.	Blepharisma	lateritia	3
241.	"	undulans	1	..	2	6	..
242.	Bursaria	viridis	1
243.	Carchesium	lachmanni	24	1	1	..
244.	"	polypinum	5	3	..	2	1
245.	Chaenia	teres	2	2	2	..
246.	Chilodonella	caudatus	1
247.	"	cucullulus	20	2	4	5	8	3	27	11
248.	"	uncinatus	13	7	4
249.	Chilodontopsis	crenula	9
250.	Cinetochilum	margaritaceum	36	4	3	4	4	6	10	9
251.	Codonella	cratera	2	5
252.	Coenomorpha	medusula	6	12	2
253.	Coleps	amphacanthus	1
254.	"	hirtus	21	1	1	..	7	7
255.	"	octospinus	2
256.	Colpoda	aspera	2	..	10	5	2	..
257.	"	inflata	3	4	9	3	1
258.	Colpidium	campylum	3	9	1	2	5
259.	"	colpoda	3	1	4	2	7	6	8	3

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS
(Continued)

Species Present	Frequency of Occurrence							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
260. <i>Cristigera spinifera</i>	3
261. <i>Cyclidium glaucoma</i>	37	7	4	15	14	6	32	30
262. <i>Cyrtolophosis mucicola</i>	3
263. <i>Dactylochlamys</i> sp.....	2	..	2
264. <i>Drepanomonas revoluta</i>	3	..	3	1
265. " <i>sphagni</i>	2
266. " <i>viridis</i>	5
267. <i>Didinium nasutum</i>	1	4	1
268. <i>Dileptus anser</i>	4	1	..
269. " <i>gigas</i>	4	1
270. <i>Dysteriopsis minuta</i>	1	2
271. <i>Epistylis plicatilis</i>	5	..	13	27
272. <i>Euplotes charon</i>	3	4	4	3
273. " <i>harpa</i>	3	2	1	..	9	3
274. " <i>patella</i>	3	2	2	1
275. " <i>plumipes</i>	1	1	..
276. <i>Frontonia acuminata</i>	5
277. " <i>leucas</i>	14	1	..	2
278. <i>Glaucoma frontata</i>	5	1
279. " <i>scintillans</i>	7	25	6	18	17
280. <i>Halteria grandinella</i>	17	8	6	4	1	..	1	..
281. <i>Hexotrichia caudatum</i>	1	4
282. <i>Holophrya discolor</i>	11	..	2	2	1	2
283. " <i>nigricans</i>	5	1	2
284. " <i>ovum</i>	2
285. " sp.....	12	13
286. <i>Lacrymaria coronata</i>	4
287. " <i>olor</i>	3	3
288. <i>Lagynus simplex</i>	1	..	1	..	2	..	1	2
289. <i>Lembadion bullinum</i>	1
290. " <i>conchoides</i>	9
291. <i>Lembus infusionum</i>	5	1	..	3	2	..	4	1
292. " <i>pusillus</i>	1	2	1	..	1	1
293. <i>Lionotus cygnus</i>	1	1
294. " <i>fasciola</i>	16	..	1	2	8	2	21	20
295. " <i>lamella</i>	6	2	7	9
296. " <i>wrzesniowskii</i>	6	1
297. " sp.....	16	2	6	8	11
298. <i>Loxocephalus granulatus</i>	16	4	3	1	3	1
299. <i>Loxodes alveolata</i>	1	2	..
300. " <i>magnus</i>	1
301. " <i>rostrum</i>	6	1	..	2	4	1
302. <i>Loxophyllum maleagris</i>	1	..	2	6
303. " <i>rostratum</i>	2	..	1
304. <i>Mesodinium pulex</i>	8	3
305. <i>Metopus contortus</i>	10	3	1
306. " <i>sigmoides</i>	8	..	12	..	10	22	3	..
307. <i>Microthorax sulcatus</i>	4	..	2	..	1	..	8	12
308. <i>Nassula aurea</i>	2	..	1	2
309. " <i>ornata</i>	9	1
310. <i>Onychodromus grandis</i>	1	1	..
311. <i>Ophrydium versatile</i>	1
312. <i>Opercularia</i> spp.....	2	6	42	36

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS
(Continued)

Species Present	Frequency of Occurrence							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
313. <i>Oxytricha chlorelligera</i>	10
314. " <i>fallax</i>	12	2	3	1	6	2	13	3
315. " <i>spp.</i>	22	4	6
316. <i>Paramecium bursaria</i>	4	1	..
317. " <i>caudatum</i>	10	27	1	12	2
318. " <i>putrinum</i>	1	5	3	8	1
319. " <i>trichium</i>	4
320. <i>Plagiopyla nasuta</i>	5	1	6	2	2	..
321. <i>Pleuronema chrysalis</i>	3	1	..	1	4	..
322. <i>Pleurotricha lanceolata</i>	2	1	..	2	..
323. <i>Prorodon griseum</i>	2	5	..
324. " <i>teres</i>	4	2	3	..
325. <i>Rhopalophrya crassa</i>	1	..	2	1	..
326. <i>Saprodinium putrinum</i>	8	..	5	..	12	28	1	..
327. <i>Spathidium spathula</i>	4	1	1	..	1	..	3	7
328. <i>Spirostomum ambiguum</i>	8	5	..	2	..
329. " <i>teres</i>	2	1	..	3	1
330. <i>Spirozoona caudatum</i>	2
331. <i>Stentor coeruleus</i>	9
332. " <i>polymorphus</i>	13	1	2	..	7	..
333. <i>Stichotricha secunda</i>	2	3	1	..
334. <i>Stylonychia mytilus</i>	6	..	1	2	15	..	2	6
335. " <i>pustulata</i>	7	12	..	9	10
336. <i>Strombidium gyrans</i>	13	1	2
337. <i>Placus luciae</i>	6
338. <i>Tintinnopsis fluviatile</i>	1	1
339. <i>Trachelius ovum</i>	1
340. <i>Trachelocerca phoenicopterus</i>	2	5
341. <i>Trichopelma sphagnetorum</i>	1
342. <i>Trimyema compressa</i>	1	..	2	27	1	..
343. <i>Trochiliopsis opaca</i>	1	..	2	5
344. <i>Urocentrum turbo</i>	7	4	2	..
345. <i>Uroleptus piscis</i>	1	5	..
346. <i>Uronema marina</i>	13	3	1	..
347. <i>Urotricha farcta</i>	12	3	1
348. <i>Vorticella campanula</i>	5	3
349. " <i>nebulifera</i>	2
350. " <i>microstoma</i>	20	6	8	17
351. " <i>sp.</i>	31	6	7	8	26	10
Number species occurring:								
in each habitat.....	289	108	103	+	148	98	136	99
in 33% of samples.....	16	11	5	2	15	12	20	15
in all habitats.....	12
in first 3 habitats.....	41
in last 4 habitats.....	57
in habitats 5 and 6.....	88

(+) Does not include any marine protozoa except those which have also been found in one of the seven freshwater habitats.

ably expected to occur as frequently as once in three samples of that type. For the perhaps less variable environment of activated sludge plants about 16 per cent of the species could be expected as often, at least in the active state. Table 1 emphasizes some of these general relationships to environment for the species considered by attempting to show frequency of occurrence correlated with numerous examinations of particular environments.

SEASONAL FACTORS

Temperature changes and changes in intensity or amount of light available for photosynthesis are difficult to separate from other seasonal effects. These include snow over ice on lakes or pools; increased volume of water in pool or stream by seasonal rainfall or melting snow, which diminishes organism concentration therein; shortening the age of water by rapid run-off following rainfall; and the manifold effects of erosion silt in flood waters such as changing chemical composition of the water, decreasing available light, or sweeping away a normal food supply. The seasonal variation in rivers or pools might be due to any one or combination of these effects. Actual proof of seasonal variation in numbers of protozoan species or individuals is quite rare in the literature.

Wang (1928) studied the seasonal distribution of protozoa in a pond in Philadelphia and listed a number of temperature effects, some of them direct. He decided that certain species were eurythermic, others thermophilic, and so on. His samples were from near the surface, however, and any stratification or migration effects would have been missed.

Welch (1935) points out that disappearance of a plankton species may be only apparent, whereas the plankters are present in a body of unmodified water in some life history stage throughout the year and successive years. Interpretation of field results as directly due to temperature should consider the modification to which the body of water is subject. Kofoid (1903) found seasonal fluctuations in river plankton, deciding they were largely due to rapidity of multiplication as the temperature increased. Reinhard (1931) also noted some such fluctuations in the upper Mississippi, but they were minor changes affecting principally chlorophyll bearing forms. It need hardly be emphasized that extreme modifications are undergone by river waters. Examination of the Ohio in August and September, 1936, revealed an abundant plankton; *Cryptomonas erosa* occurring in all samples. But in January, 1937, this organism could not be found in the silt laden flood waters of the stream, whereas it was still abundant in ponds near Cincinnati.

Crozier and Harris (1922) found a seasonal fluctuation in the numbers of protozoa present in the Plainfield, N. J., trickling filter. This fluctuation may be entirely passive with the protozoa, and due to the well-known seasonal "sloughing" of the film from the stones. I have found no such changes in the somewhat similar protozoa of activated sludge plants, which maintain a high population throughout the year. These habitats are subject to con-

siderable less modification than streams, but their temperature ranges fluctuate markedly. Viehl (1934) has recently shown by experiments in activated sludge plants that temperatures between 8°C. and 35°C. produced hardly significant changes in numbers of species and organisms. His experiments ranged from 1.5°C. to 55°C. and only the lower and upper ranges were highly effective.

I believe the most marked seasonal changes due to temperature to be quantitative. In 1932 and 1933 I made some observations on a small pool in South Mountain Reservation near Milburn, N. J., and in 1934 Fronczak (1936) made a careful study of this pool from January 9th to April 30th. Its greatest modification in that time was largely due to temperature. This uncontaminated pool "20 feet long, and 5 feet wide at its widest part—17 to 18 inches deep in the center" is fed by seepage, and while occasionally flushed out by a rain or thaw, quickly resumes its normal appearance, so that its greatest yearly changes are probably those of temperature and an annual accumulation of leaves in the fall. Its pH remained close to 6.8 at all times and its iron content high. The first examination in the fall of 1932 showed 78 species, but 171 were recorded by Fronczak in his intensive study in 1934. During the time he worked the temperature ranged between 2°C. and 12°C., usually below 10°. There was constantly a large protozoan population present; often the water was green with chlorophyll bearing forms. At 2° there were 28,000 individuals per cc. comprising 40 species, 77 per cent being chlorophyll bearers. At a temperature of 4°, 175,000 per cc. were found. Numbers showed a definite rise as the temperature increased, but the number of species changed only slightly, and the summer species counts (mine) never exceeded those of winter; furthermore the summer and winter species list was about the same. The maximum number ever observed at one examination was 66, a winter count. During 3 years this pool showed no decided seasonal changes.

I have made substantially the same observations on a larger, spring-fed pond at Metuchen, N. J., where approximately as large a species list was obtained from beneath two inches of ice, when the temperature was about 4°C., as in late summer. Such observations indicate that seasonal effects must be very carefully evaluated.

There are undoubtedly certain species which react to high or low temperatures by encystment or some other alterations in the life history. Noland (1925) found certain ciliates which decidedly favored low temperatures and I have found this to be true of *Strombidium gyrans*. If the principal food of a protozoan species consisted of certain green flagellates, it might disappear except during the summer months when such forms as Pandorian or Gonium tend to be most abundant.

It is probable, however, that the majority of protozoa enjoy a broad range of temperature toleration if temperatures change gradually. It seems that the chief influence of low temperatures is to slow up metabolism, hence

division rate, while high temperatures accelerate it. I have proved experimentally that *Colpoda inflata* divided about three times as fast at 27°C. as at 10°C. Temperatures below 10°C. and above 30°C. probably greatly affect the numbers of individuals present, but not the number of species.

HYDROGEN ION CONCENTRATION AND CHEMICAL COMPOSITION AS LIMITING FACTORS

Table 2 gives a list of twenty-six species of protozoa found in a variety of habitats during two years work by Rudolfs and Lackey (1929) endeavoring to explain the breeding of mosquitoes in specific places. The most striking character of the data is the lack of any apparent correlation between the species found and the chemical composition of the water, the various factors noted. Indeed so wide are the ranges of pH, CO₂, CO₃, Cl, and SO₄ at which some of the species occur that one might be tempted to ask if those species are not possibly independent of these usually occurring environmental factors. For example, Saunders (1925), Pruthi (1927), Darby (1929), and Phelps (1934) have reported widely divergent findings as to the tolerated pH range for *Paramecium* and the optimum pH. Phelps was unable to account for the observed differences. Pruthi did not give the species of some genera other than *Paramecium* with which he worked, and different species of the same genus frequently react differently to similar conditions. Indeed much recent work of this sort has most unfortunately not given the species worked with, but only the genus. In a natural environment the pH may undergo extensive changes in relatively short periods of time, and if a species is unable to accommodate itself to these changes, it must die out or perhaps encyst; Peterson (1928) reports that suddenly lowering the pH from 7.4 to 6.5 by adding 0.5 per cent lactic acid "killed all of the active individuals and probably many of the encysted" *Euglena polymorpha*, but that after 18 days they reappeared, presumably from cysts, at a pH of 6.6 and thereafter adapted themselves to the medium, increasing greatly in numbers. In Table 2, 193 determinations have been made for 26 species of protozoa, and the lowest pH is 2.9 and the highest 8.0.

In an examination of another group of more than 200 field samples, *Trachelomonas volvocina* and *T. hispida* were found in 41. For these 41 samples the range of pH was 4.6 to 8.0; CO₂, .8 to 13.2 p.p.m.; CO₃, 1.0 to 297.0 p.p.m.; Cl, 0 to 40.0 p.p.m.; and SO₄, 0 to 1016 p.p.m. The maximum occurrence of these flagellates was at pH 6.4; but none were found at pH 6.3. If we plot their distribution and that of *Arcella vulgaris*, *Aspidisca costata*, *Cyclidium glaucoma*, *Halteria grandinella*, and *Oxytricha fallax* against the field pH records at which they were observed, no unimodal curve is obtained. Instead it is apparent that they occur at a wide range of hydrogen ion concentration; that a very large number of observations would be necessary to establish an optimum; and that the pH factor is probably inseparable from other factors.

TABLE 2. THE RANGE OF pH AND CERTAIN CHEMICAL SUBSTANCES IN FIELD
SAMPLES CONTAINING VARIOUS PROTOZOATop figure the minimum, bottom figure the maximum.
Results in parts per million

Organisms	Number samples in which found	pH	CO ₂	CO ₃	Cl	SO ₄	Ca & Mg	Al	Tot. Sol.	Vol. Mat.	Fe
1. Actinophrys sol.....	7	2.9 6.7	2.2 6.0	0.0 36.9	0.0 65.0	0.0 1644.0	0 0	0 99	tr tr	tr tr	0 85
2. Actinosphaerium eichorni.....	3	4.7 6.7	6.0 26.4	5.2 25.0	0.0 296.0	4.0 1570.2	0 0	tr tr	tr tr	tr tr	0 0
3. Arcella vulgaris.....	20	2.9 7.4	2.0 44.0	0.0 225.7	0.0 19.84	0.0 1356.3	0 7	0 99	tr 9	tr 80	0 85
4. Clathrulina elegans.....	3	5.4 6.9	3.5 9.6	9.6 19.2	7.95 972.0	10.0 65.7	tr tr	tr tr	tr tr	tr tr	tr tr
5. Euglypha alveolata.....	8	4.2 6.7	0.0 9.6	2.6 25.0	0.0 7.95	0.0 65.7	tr tr	tr tr	tr tr	tr tr	tr tr
6. Trinema lineare.....	5	4.9 6.7	0.0 9.6	2.6 25.0	0.0 7.95	14.0 48.0	0 tr	tr tr	tr tr	tr tr	0 tr
7. Chilomonas paramecium.....	9	4.6 7.4	2.0 13.2	2.6 102.0	0.0 39.8	tr 103.5	tr 7	tr tr	tr 110	tr 80	tr tr
8. Entosiphon sulcatum.....	3	5.9 7.4	2.0 8.5	8.4 58.0	0.0 17.7	80.0 73.8	tr tr	0 tr	70 tr	50 tr	0 tr
9. Euglena acus.....	3	4.9 6.9	0.8 10.5	5.3 27.7	7.95 11.7	80.5 159.8	tr tr	tr tr	tr tr	tr tr	tr tr
10. Euglena mutabilis.....	3	2.9 7.3	5.2 tr	0.0 45.0	tr 65.0	256.0 1636.3	0 0	0 tr	0 tr	20 tr	100 85
11. Euglena polymorpha.....	6	7.0 8.0	4.0 11.4	2.19 135.0	0.0 91.0	0.0 935.4	tr 18	0 tr	0 680	100 640	0 18
12. Euglena viridis.....	5	4.6 7.5	2.0 11.4	80. 6.0	0.0 29.7	80.0 1636.3	0 tr	0 45	70 tr	50 tr	0 18
13. Gonium sociale.....	3	6.1 7.5	2.0 tr	1.0 135.0	0.0 tr	0.0 1016.0	0 800	0 tr	160 5200	140 4200	0 tr
14. Mallomonas caudata var. macrolepis.....	6	4.6 6.4	3.5 26.4	3.3 21.0	0.0 45.6	41.0 1636.3	tr tr	tr tr	tr tr	tr tr	0 tr
15. Menoidium incurvum.....	6	4.6 7.5	2.0 135.0	3.6 58.0	0.0 7.9	8.0 259.7	0 tr	0 tr	tr 520	tr 420	0 tr
16. Peranema trichophorum.....	8	5.2 7.3	2.2 13.0	4.5 72.0	0.0 39.7	14.0 101.9	0 tr	tr tr	tr 680	tr 640	0 tr
17. Rhipidodendron splendidum.....	8	4.9 6.7	1.7 10.0	9.6 25.0	0.0 12.0	tr 174.0	0 tr	0 tr	tr 900	tr 600	tr tr
18. Synura uvella.....	8	4.9 7.3	0.4 9.6	2.6 45.0	tr 11.7	23.0 259.7	0 tr	0 tr	0 tr	200 tr	100 tr
19. Aspidisca costata.....	19	4.6 7.3	0.0 15.8	2.4 153.6	0.0 65.5	70.0 36638.0	0 tr	tr 580	tr tr	tr tr	tr 120
20. Chilodonella cucullulus.....	7	4.8 7.4	2.0 29.9	1.0 229.6	0.0 60.0	0.0 2038.0	0 7	0 tr	tr 7000	tr 5000	0 tr
21. Coleps hirtus.....	7	5.5 7.4	2.0 29.9	6.0 229.6	tr 60.0	tr 2729.0	tr 70	0 tr	70 110	100 80	0 tr
22. Cyclidium glaucoma.....	11	2.9 8.0	0.0 9.6	0.0 219.0	0.0 91.0	0.0 256.0	0 18	0 9	110 900	60 160	0 85
23. Frontonia leucas.....	5	4.6 7.5	2.4 9.6	3.6 25.0	0.0 7.9	0.0 208.0	0 114	0 248	tr tr	tr tr	0 52
24. Halteria grandinella.....	11	4.2 7.5	2.6 28.1	2.4 225.7	0.0 29.0	0.0 1636.3	0 tr	0 172	90 tr	60 tr	0 tr
25. Microthorax sulcatus.....	5	5.8 8.0	2.2 6.0	6.0 297.0	0.0 7.9	14.0 108.5	0 13	0 tr	0 tr	tr 24	tr 18
26. Oxytricha fallax.....	14	4.6 7.5	2.0 29.9	2.4 53.6	0.0 91.0	0.0 2729.0	tr 18	0 tr	70 6800	50 6400	0 tr

Noland (1925) has made similar observations on *Aspidisca costata*, *Cyclidium glaucoma*, and *Halteria grandinella*. His alkaline values exceed those recorded here in each case; 9.8 for *Aspidisca* and *Halteria*; 8.6 for *Cyclidium*. He did not note an optimum pH for any of the three, either in the field or in laboratory cultures, but averaged the pH values and concluded that "it is doubtful whether the pH exerts any direct influence on ciliate distribution within the range observed." This assumption is in complete accord with the results of this survey as far as the twenty-six species herein dealt with are concerned.

Such a conclusion might well be applied to the chemical values shown by the analyses. Wide ranges of CO_2 , CO_3 , Cl, and SO_4 , are found to be tolerated. If any inference is to be drawn from the data, it is probably that the species concerned are independent of the limits of the above chemical factors likely to occur in stagnant water. This is borne out in part by the fact that 13 of the 26 organisms in Table 2 were found by Edmondson (1920) in Devils Lake waters, where the salts concentration approximates that of the sea, but with very high sulphates rather than chlorides; and that 10 of these 26 species were found in the Atlantic Ocean. Kofoid (1903) found that there was little correlation between chemical changes and seasonal fluctuations of the plankton in the Illinois River, and Weston and Turner (1917) noted that a sewage-polluted stream returned to a normal biological condition before its normal chemical condition was restored.

The 41 samples in which *Trachelomonas volvocina* and *T. hispida* occurred were taken from 12 stations over a period of two years. Despite extensive variation of the chemical makeup of the pools the organisms persisted. Fine (1912) is of the opinion that extensive knowledge of the chemical makeup of the environment would still produce only the most superficial correlations, and he shows that either titratable acidity or protozoan sequence may vary widely in hay infusions without appreciably affecting the course of the other, and a study of these data apparently indicates that such is the case for these two organisms.

The wide variations in amounts of salts and radicals present in the sample suggests that a balance is produced in the environment between various salts and radicals, and it is this balance which enables the protozoa to be tolerant of wide fluctuations in pH range.

Temperature variations, dissolved oxygen, light intensity, and such factors are not necessarily significant, for the 41 samples were all from natural pools, streams, or ditches. In general the chemical analyses justified the pH values and indicate that there were no large quantities of other, possibly toxic, ions present. Some conspicuous exceptions occurred as in sample 19, where there were small values for CO_2 , CO_3 , and Cl, but the highest recorded value for SO_4 , 259.7 and a pH of 5.5. It is not known what other salts were present to aid the balancing action, but there were numerous protozoa of

nine species in this water, strengthening the argument that the buffering action of the salt balance accounts for wide tolerance of pH.

FOOD AS A LIMITING FACTOR

Sandon (1932) believes that food is largely the controlling factor for protozoa. If so, one might reasonably expect a large variety of bacteria-eating protozoa to be present in the aeration chambers of a sewage disposal plant or in its trickling filters. Table 4 gives a list of species exceeding 100 per cc., and numbers present in the aeration chambers or trickling filters of three disposal plants on several dates. The numbers of individuals are large, but numbers of species disappointingly small, even if those occurring in small numbers be added. *Paramecium* is usually absent from the samples at the Cincinnati and Tenaflay plants although one or more species may occasionally be found in them and in nearby polluted waters. Yet there are bacteria present which Phelps (1934) and others have shown to be food for it. There is abundant oxygen, air being continually forced through the sludge. The pH values are constantly near neutrality and no large quantities of trade wastes are present. Any attempted conclusion from this table would be exactly counter to the idea that food is the limiting factor, for here where there is an abundance of it, other factors tend to sharply restrict the protozoan fauna. *Strombidium gyrans* feeds largely on *Chromulina ovalis*, and when the numbers of these drop in the Reservation Pool, *Strombidium* also becomes scarce, but such an observation is not proof of cause and effect. It has been stated that the abundance of organisms of one type found in a given situation is in a general way inversely proportional to the diversity of kinds, but there is perhaps the potential for supporting an enormous population in these three sewage disposal plants; yet neither in types nor numbers of individuals do the protozoa seem to approach their limit there. The Plainfield disposal plant over a period of time contains a much greater number of species in its trickling filter, as shown by Table 1, Column 7. This list is incomplete, not all the species of small flagellates having been identified; also some species which occur only once or twice in a year are not given in the table, but it certainly includes those which occur with significant frequency. Apparently all sewage disposal plants which treat largely domestic wastes have approximately the same fauna. Lists of protozoa occurring in other New Jersey disposal plants as Chatham, Red Bank, Barrington and Collingswood have shown substantially the same organisms, while similar faunas are reported from Decatur, Illinois, by Agersborg (1929); from Leipsic by Viehl (1934); from State College, Pa., by Lindsay (1930); and Ames, Iowa, by Frye and Becker (1929). Total numbers may vary considerably in different plants and at different times, but the species list does not vary a great deal. While the list includes many common species, it also includes some species rarely found elsewhere; on the other hand a number of species common to natural waters or stagnant pools are not found in such

plants, as will be seen by comparing Columns 7 and 8 with Column 1 in Table 1. This fact and the wide occurrence of similar species in sewage disposal plants might indicate that such plants offer an environment whose limits are well fixed. Decided variations occur within these limits, but a balance is maintained, and the organisms are largely independent of the fluctuations as far as existence is concerned. If in addition to their domestic wastes, large quantities of alkalis, acids or trade wastes of various kinds are introduced into the influent, the numbers and kinds of the protozoa will be greatly affected, and the efficiency of the plant possibly impaired.

Since there is certainly an abundance of food for bacterial feeders in trickling filters and activated sludge chambers, as is indicated by the great reduction of bacteria in these places, it might be expected that pH or chemical substances would account for the differences in fauna. Such is not the case; sewage is normally a very dilute mixture, and in aeration chamber or trickling filter normally contains abundant dissolved oxygen, while its pH and chemical composition are comparable to the field water samples analyzed in Table 2. And yet its most characteristic protozoon, Opercularia, was not recorded once in the 68 field samples of Table 1, while other faunal differences almost as great exist. Evidently its organisms manifest highly specific food requirements, or it possesses minute quantities of restrictive decomposition products; or its physical characteristics as a substrate are restrictive.

Where an organism is a highly selective feeder as *Didinium nasutum* which feeds on *Paramecium*, food can easily be a controlling factor. But where feeding is not selective, as seems to be the case with so many protozoa, food ceases to be restrictive.

POSSIBLE LIMITING FACTORS IN IMHOFF TANKS

In sewage disposal plants, both sprinkling filters and aeration chambers contain quantities of putrescible matter and large numbers of bacteria, so that both saprozoic and holozoic animals should thrive. One not acquainted with methods of sewage disposal might suspect oxygen depletion or hydrogen sulfide accumulation as limiting factors. Neither applies to these parts of a plant, however, because air is intentionally supplied in both cases. In Imhoff and septic tanks there is typically no oxygen and there may be H_2S ; putrescible matter and bacteria are very abundant here also. But the protozoan fauna is very limited both as to numbers of species and numbers of individuals. Column 6 of Table 1 is a list of the species found by me (1925) in some numbers in the Imhoff tanks at Plainfield, N. J., and other places. These may not be present at all times and it is rare that they reach high numbers, but four species of ciliates, eight species of flagellates, and one rhizopod occur with some constancy in the tanks. These 13 species are different from those of the filter beds and their numbers are small. Careful studies of these tanks (1926) indicate a fauna which rarely exceeds 20,000 per liter, when the tanks are functioning normally. Extreme variations occur

when they function poorly, but their fauna may dwindle practically to the vanishing point, a condition which never occurs in the filter beds or in the aeration tanks. The tank protozoa therefore constitute a group very restricted by environment. Experiments (1932) have shown that they are either facultative or obligatory anaerobes. For the latter the presence of oxygen is a limiting factor. *Trepomonas agilis*, *Metopus sigmoides*, *Saprodinium putridum*, *Trimyema compressa*, with a small unidentified Holophyra are certainly in this category, and probably *Hexamitus inflata* and *Mastigella simplex*. These thrive in Novy jars from which the oxygen has been exhausted. But if H_2S accumulates, *Metopus* will die out, while the remaining four endure considerable concentrations of this gas. None of the other Imhoff tank forms listed exhibit any marked tolerance for H_2S , and while some of them will thrive in Petri dish cultures under a thick film of paraffin oil floating on the water, if the oil seals the dish tightly by forming a film between the rim and the cover so that H_2S accumulates they quickly die out.

Many protozoa appear to stand some degree of oxygen depletion. I have grown many species under films of paraffin oil during the last three years; *Entosiphon sulcatus* grows in enormous numbers whether with or without the film of paraffin oil, but no mass cultures of *Distigma proteus* were procurable except in media under a cover of paraffin oil despite the fact that this organism is occasionally met with in the field. Thriving cultures of *Holosticha rubrum*, a large red marine ciliate, have been maintained for six months, with the best cultures growing under oil. Coste (1917) has shown that oils do not exclude oxygen from water and while oxygen is more soluble in petroleum (paraffin oil) than in water, (.028 volumes per volume of water, as compared to .202 volumes per volume of petroleum at $20^\circ C.$), there is apparently a small transfer of oxygen across the surfaces in contact, the oxygen below soon being partially depleted.

Oxygen exhaustion, then, seems to be a limiting factor if sufficiently great; a high percentage of H_2S seems to be another. In the field, however, these two conditions are rarely met. Noland (1925) noted that *Colpoda steinii*, *C. cucullus*, *Glaucoma scintillans*, *G. pyriformis*, and *Paramecium caudatum* were tolerant of a very low oxygen content. Of these only *G. scintillans* has ever been met with in the Imhoff tanks, although the others can be cultivated in infusions under paraffin oil. Evidently they are not tolerant to H_2S or more probably methane. Although albumen digesting bacteria (H_2S producers) are present in the tanks the concentration of H_2S in the tank gases is usually not greater than 0.1 per cent. Methane is usually about 70.0 per cent; CO_2 20.0 per cent to 25.0 per cent and sometimes CO about 0.3 per cent in the tank gases. Under acid conditions, the tanks foam and small amounts of hydrogen appear. When this occurs, very large numbers of small flagellates, principally *Trepomonas agilis*, but also some *Tetramitus decissus* and *Hexamitus inflatus* make their appearance. The hydrogen can hardly be called the stimulus here, but the lack of oxygen

TABLE 3. LIST OF PROTOZOAN SPECIES WHOSE NUMBERS APPROXIMATED OR EXCEEDED 100 PER CC. IN THE TRICKLING FILTERS AND AERATION CHAMBERS OF THREE SEWAGE DISPOSAL PLANTS

Organism		Plainfield, N. J. Trickling filter ¹						Tenafly, N. J. Activated sludge						Cincinnati, Ohio Activated sludge			
		9-9-22	1-1-23	5-5-23	10-2-24	10-5-24	11-7-24	7-8-33	7-10-33	7-12-33	7-26-33	8-1-33	8-31-33	8-3-36	8-24-36	8-31-36	9-18-36
<i>Sarcodina</i>	<i>Amoeba</i> spp. (2).....	1000	2000	1500	9700	2200	4000	18000	13200	28100	64400	61400	13000	300	1500	700	500
	<i>Arcella</i> spp.....	4000	2000	3000	4700	6500	7000	7000	200	200	200	200	200	2300	400	100	600
	<i>Chlamydomorphys stercorea</i>						700							100	400		100
	<i>Centropyxis aculeata</i>								200					4300		200	
	<i>Cochliopodium bilimbosum</i>	1000	2000	100	400	2900	1000					100		300	100	1500	
	<i>Diffugia pyriformis</i> and <i>lebes</i>	1500		2000	5000	1400	600							100			
	<i>Euglypha alveolata</i> and <i>ciliata</i>						5000							100			
	<i>Nuclearia simplex</i>													100			
	<i>Trinema lineare</i>				1100									100			
	<i>Maatophora</i>	<i>Anisonema ovale</i>				400			400						2900		
<i>Distigma proteus</i>						100								400		300	
<i>Entosiphon sulcatus</i>					400	100	1000			200					100		
<i>Euglena</i> sp. (3).....						500	500	1200	400	600	400	200		500	700		100
<i>Infusoria</i>	<i>Peranema trichophorum</i>	15000	30000	20000	63300	67000	18000							100			100
	<i>Minute flagellates</i> (4).....																
	<i>Aspidisca costata</i>	1000	8000	1000	4700	5800	4000	9200	7700	6700	9600	10700	200	300	1500	700	500
	<i>Blepharisma undulans</i>				400												
	<i>Chilodonella cucullulus</i>	200	1500			1400	300								600	100	100
	<i>Chilodonella uncinatus</i>																
	<i>Cinetochilum margaritaceum</i>																
	<i>Colpidium campyla</i>		5000		1400	1000					600		200				
	<i>Colpoda</i> sp.....	1000	5000	1000													
	<i>Cyclidium glaucoma</i>						700									100	100
	<i>Frontonia leucas</i>		1000														
	<i>Holophrya nigricans</i>																
	<i>Lionotus fasciola</i>				3300	13000	600		200	200		200		100	1500	1700	1500
	<i>Lionotus</i> sp.....				58800	1200			1000	2100	1500	200	200				
	<i>Loxophyllum rostratum</i>	1500															
<i>Opercularia</i> spp. (5).....	80000	70000	50000	96600	108000	70000	2300	7800	10400	8800	13600	13000	1300	6300	1400	4500	
<i>Oxytricha fallax</i>				400	500	100											
<i>Paramecium caudatum</i>	3000	30000			700	1000		400									
<i>Paramecium putrinum</i>																	
<i>Pleuronema chrysalis</i>																	
<i>Spirostomum ambiguum</i>																	
<i>Stylonychia pustulata</i>																	
<i>Vorticella</i> spp.....	100	2000	100						200						100	100	600
<i>Acinetia grandis</i>	100	1000	3000	400				800	1700	800	600	200	2200	200	100	100	
<i>Podophrya fixa</i>																	

(1) Hausman gives only genera; species given I subsequently found at Plainfield.

(2) Includes four species *Amoeba* and three of *Vahlkampfia*.(3) Colorless, either *gracilis* or *quartana*.

(4) Several genera, but in hasty counting no careful identification can be made.

(5) Includes also some species of *Epistylis*.

and the presence of the other gases certainly combine to restrict the fauna to the organisms noted.

ASSOCIATIONS

Despite the apparently cosmopolitan distribution of many protozoan species, any particular habitat is likely to be characterized by a certain group of protozoa whose occurrence therein is determined by a number of environmental factors including possibly associations of certain organisms. The food associations of *Strombidium gyrans* with *Chromulina ovalis* or *Didinium nasutum* with *Paramecium caudatum* are of this nature. But more evident groupings are encountered if one studies a certain habitat over a period of time. The Reservation Pool studied by Fronczak (1936) and myself, showed practically the same list of species in 1932, 1933 and 1934. Many of these occurred sporadically but the bulk of its population, at times a very large one, was made up of about 60 constantly recurring species. Sixteen of the organisms of Table 2 and 18 of those in Table 5 occurred almost constantly in it. But whereas only 6 per cent of the protozoa in Column 1 of Table 1 might be found in one out of three random samples, 42 per cent of the species from this pool were found in one third of the samples, i.e., there was a marked association of species. The practically constant occurrence of organisms such as *Chromulina ovalis*, *Chroomonas setoniensis*, *Strombidium gyrans*, *Balanitozoon agile*, *Oxytricha chlorelligera*, *Dileptus gigas*, *Glaucoma frontata*, *Placus luciae* and *Spirozona caudata* is noteworthy, for most of these organisms do not occur commonly, and rarely together, so far as my field experience indicates. While such constant associations may be readily recognized, they give little indication of causative conditions, but they do point to a relative sameness of those causative conditions.

PROTOZOA AS ECOLOGIC INDICATORS

From a study of the data presented herein, some conclusions may be drawn as to the value of certain protozoa for indicating the degree of pollution of natural waters. Kolkwitz and Marsson (1909), Forbes and Richardson (1913), Purdy (1922, 1930), Noland (1925), and others have already classified many species ecologically in respect to pollution, and Whipple (1927) gives a table of the species so classified.

Pollution usually means the presence of sewage, but it might mean the presence of offensive odors and tastes, a high *B. coli* count, depletion of oxygen saturation, or a combination of these, from other causes. To be valuable as indicators of purity, a protozoan species should not thrive under oxygen depletion or extremes of pH; it should be quite susceptible to unusual salts, gases, or organic substances in the water. Some organisms will occur in too great numbers under a variety of conditions to be indicators. *Euglena polymorpha* occurred abundantly in 1924 at 6 stations under the following conditions:

Nature of Water	pH	CO ₂ p.p.m.	CO ₃ p.p.m.	SO ₄ p.p.m.	Ca & Mg p.p.m.	Al p.p.m.	Total Solids p.p.m.	Vol. Mat. p.p.m.	Fe p.p.m.	Cl p.p.m.
Polluted.....	7.5	4	219	Tr.	180	00	240	160	Tr.	91
Polluted.....	7.4	8	102	00	70	Tr.	110	80	00	Tr.
Polluted.....	8.0		297		130	00	00	240	180	40
Clean.....	7.3		72		Tr.	Tr.	680	640	00	00
Clean.....	7.5		135		Tr.	Tr.	520	420	00	Tr.
Clean.....	7.5		39		80	00	250	280	00	00

The high pH values here might indicate tolerance for alkalinity, but equally large numbers of this species have been encountered in the clean but acid waters from a cedar swamp. Two hundred and seventy thousand (270,000) *Euglena mutabilis* per cc. have been found in polluted waters at a pH of 2.9 and with ferrous iron as high as 850 p.p.m., but large numbers of the same form also occurred in clean water at a pH of 7.3 and with but a trace of iron present. If we compare the chemical environments of these two *Euglenas* with that of *Euglena oxyuris* as shown by Senior-White (1928), it becomes apparent why conclusions cannot be based on genera but must be applied to species. He found Euglenids "mainly *E. oxyuris*" present in large numbers only in the absence of free CO₂, i.e. at a pH greater than 8.4. The pool under investigation was a foul one, high in ammonia and phosphates. These species and the two species of *Trachelomonas* referred to in Table 2 clearly show that little can be judged of the state of the water by their presence. Not only do they fail to indicate purity or pollution, but fail to indicate the presence or absence of iron, although Euglenidae are generally believed to show a preference for iron-containing waters.

On the other hand, *Euglena acus*, *Euglena agilis*, and *Euglena gracilis* may well serve as indicators of heavy organic pollution, for all three thrive where putrescible compounds, such as are found in sewage or in decaying plant infusions, are abundant. But it is only when they are colorless that they indicate such conditions; they apparently do not lose their chlorophyll in relatively clean waters, and specimens brought in from the field are usually green. Those from sewage treatment plants, however, are usually colorless, and when *Euglena acus* is inoculated into a strong hay infusion, it may reproduce rapidly with no vestige of chlorophyll. Only a few chlorophyll bearing flagellates are peculiar to excessively polluted waters. While several commonly occurring green flagellates are often referred to as characteristic of septic or polluted waters, it is their numbers which are significant more than their presence. *Euglena viridis* is so classified (vide Whipple), but according to Table 1 it occurred in about 44 per cent of the clean water samples.

In 1925, seventy-seven samples were taken from unpolluted pools, beginning March 16 and ending October 16. The pH was taken for each sample, and determinations made of CO₂, CO₃, Cl, and SO₄. The following list of species occurred in sufficient numbers to be listed as oligosaprobic forms:

<i>Actinophrys sol</i>	In 4 samples
<i>Clathrulina elegans</i>	In 2 samples
<i>Englypha alveolata</i>	In 4 samples
<i>Trinema lineare</i>	In 3 samples
<i>Chilomonas paramecium</i>	In 6 samples
<i>Entosiphon sulcatus</i>	In 4 samples
<i>Euglena acus</i>	In 4 samples
<i>Menoidium incurvum</i>	In 5 samples
<i>Peranema trichophorum</i>	In 6 samples
<i>Rhipidodendron splendidum</i>	In 5 samples
<i>Synura uvella</i>	In 7 samples
<i>Trachelomonas hispida</i>	In 17 samples
<i>Coleps hirtus</i>	In 3 samples
<i>Cyclidium glaucoma</i>	In 5 samples
<i>Halteria grandinella</i>	In 6 samples
<i>Microthorax sulcatus</i>	In 4 samples

Now these species of *Chilomonas*, *Entosiphon*, *Menoidium*, *Peranema*, *Coleps*, *Cyclidium*, and *Microthorax* also occur in sufficient numbers in the sludge chambers of sewage disposal plants where decomposition of organic matter is taking place, to be classified as pollution forms. If, however, we look for them in Column 5 of Table 1, it is seen that their occurrence, excepting *Cyclidium* in sewage polluted streams, is rare. As a matter of fact, at least three considerations must be borne in mind when accepting a protozoan species as an indicator of pollution, viz.: (1) Has it been found to occur frequently in waters known to be polluted, and rarely elsewhere? (2) Does it occur in large numbers in polluted waters, but sparsely elsewhere? (3) Does it thrive in oxygen depleted waters, or only in well aerated waters?

A few organisms readily fall into the first category above, as *Anthophysa vegetans*, or *Carchesium lachmanni*, which are practically never found elsewhere in the field. Still others fall into the second group as *Euglena viridis*, or *Paramecium caudatum*. And the third group includes forms such as *Trepomonas agilis*.

Wherever a genus is referred to an ecological classification, it must be accepted with caution, especially if the genus contains a number of sharply defined species, a condition well illustrated by some of the green flagellates. The *Euglenas* and allied forms are taken by Marsson (1909) as indicating a foul condition if abundant in pools, an idea I believe to be generally accepted yet far from accurate; the most abundant blooms of *Euglenas* I have ever seen have been those of *E. polymorpha* and *E. sanguinea*, the one on woodland and swampland pools far removed from sewage or other contamination, the other especially characteristic of open shallow ponds, especially those containing colloidal silt as freshly dug burrow pits alongside roads under construction. They occur elsewhere also, but occurrences as blooms in situations such as the above I would certainly regard as most characteristic.

Euglena viridis, classified as a polysaprobic or septic organism, occurred in 44 per cent of the clear water samples of Table 1, Column 1, and it is not the most common *Euglena* in the polluted Ohio at Cincinnati as far as present records indicate.

Actually this phase of study of the biology of polluted waters has not been investigated with sufficient exactness. A careful, specific, quantitative and qualitative comparison of clean and polluted waters with an evaluation of attendant environmental characteristics is still badly needed, and will yield very valuable information to the sanitary engineer or worker in water supplies.

SUMMARY

1. Examination of a large number of samples from a variety of habitats has shown that while protozoan species may be cosmopolitan in their distribution, nevertheless a given habitat may be prohibitive to many species because of local environmental characteristics. This is indicated by the continuance of certain species in a given locus, and the failure of other species to occur therein except sporadically.

2. Some few species are shown to occur in such a variety of habitats that they may be regarded as truly cosmopolitan.

3. Seasonal factors as temperature and light seem to affect numbers present, but few if any, species.

4. A wide range of hydrogen ion concentration and chemical composition in natural waters is shown to be tolerated by a number of species.

5. It is probable that in nature food is only a quantitative limiting factor, except for a few species whose food requirements are highly specific.

6. The various types of sewage disposal plants seem to have definite protozoan populations characterized by a large number of species in trickling filters, a much smaller number in activated sludge chambers and the smallest number in Imhoff and septic tanks.

7. Polluted streams *per se* have highly characteristic protozoan populations, but to date no critical evaluation of such a population has been given, and some erroneous generalizations have been made.

8. Protozoa should not be classified ecologically until their range of tolerance of environmental conditions is known.

9. Most species live within such a wide range of tolerance that they are valueless as indicator organisms.

10. A few species are known to be valuable indicators and the number of such species can probably be materially increased.

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FREEZING WEATHER IN RELATION TO PLANT
DISTRIBUTION IN THE SONORAN DESERT

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FREEZING WEATHER IN RELATION TO PLANT DISTRIBUTION IN THE SONORAN DESERT

INTRODUCTION

A cold wave of unusual intensity and duration invaded the Sonoran Desert in January, 1937, inflicting considerable frost damage to native plants. Temperatures were generally colder than had been experienced in 24 years, and the reaction of plants afforded evidence concerning the role of winter freezing in determining the geographical distribution of many species. Although a veritable constellation of factors is actually operative in determining distribution, a single factor may occasionally be of predominant importance. The general attitude of plant geographers to this problem has recently been summarized by Mason (1936).

Both the intensity and duration of cold are significant, and the use of minimum temperature figures alone affords a poor index of cold severity. Mean figures of low temperatures are of limited value also, as a single very cold night of a quarter of a century may do more damage to the native species than do all the moderately cold nights combined.

The amount of damage suffered by a plant is influenced by the condition of the plant at the time of freezing—whether the plant is active or dormant, turgid or dry, hardened or not, and mature or young. Certain individuals of a species are inherently more frost resistant than others. The accessory physical conditions play a modifying role—particularly soil moisture, wind, atmospheric humidity, and insolation. Frost damage to plant parts is not a sure index that the entire plant is nearing the limit of its cold endurance.

The Sonoran Desert as a geographical region has been defined by Shreve in a series of papers (see bibliography) in which he has described the distribution of many characteristic species. This natural area embraces most of the Mexican state of Sonora, southwestern Arizona, a small area in southeastern California, and most of the state of Baja California. The flora and vegetation characteristic of this region have been used as a basis in drawing the boundaries, which are shown by the dotted line of figure 1. The Sonoran Desert is not confined, therefore, to the state of Sonora, and is not to be confused with the terms "upper and lower Sonoran life zones."

In this paper we are presenting a summary and discussion of freezing weather¹ in the Sonoran Desert with especial emphasis on the January, 1937, cold wave and its damage to plants.

¹The specific meaning of the terms "freezing weather" and "frost" are somewhat in doubt. "Frost" is sometimes used to refer to the formation of ice crystals on objects during clear, calm, so-called radiation nights regardless of the thermometer reading in a shelter 5 feet above the ground. "Frost" and "freeze" both may refer to a thermometer reading of 32°F. or lower in the 5-foot shelter on radiation nights regardless of the presence or absence of ice crystals on objects. "Frost" and "freeze" are both commonly used to refer to temperature below 32°F. produced by cold waves rather than by radiational cooling. Here "freeze" is used to refer to 32° or lower minimum thermometer readings in the 5-foot shelter, and "frost" to mean the presence of ice crystals.

The authors wish to thank the many observers who have contributed information either of temperature conditions or of frost damage to plants at remote localities. These include Dr. Forrest Shreve, Mr. Jack Whitehead, Dr. I. L. Wiggins, Mr. H. S. Gentry, Dr. R. R. Humphrey, Mr. R. B. O'Neill, Dr. W. P. Cottam, Mr. Fred Gibson, Dr. T. D. Mallery, the Richardson Construction Co., Señor Ernesto Forgach, Mr. James Harding, Mr. L. L. Logan, Mr. Dean Blake, Phoenix Office of the U. S. Weather Bureau, Mr. Aguirre, Mr. L. D. Hoff, the Ferrocarril Sud Pacifico de Mexico, Señor Guillermo Munro, and Mr. Floyd Young.

SYNOPTIC ASPECT OF 1937 COLD WAVE

The following excerpt is from a letter by Dean Blake, Associate Meteorologist, U. S. Weather Bureau, San Diego, California, in which he has described the salient meteorological features of the January, 1937, cold wave:

"Disastrous freezes, that occasionally occur over the southwestern United States, invariably are the result of an abnormal southerly movement of polar air, and the cold wave that overspread the Far West during the latter part of January, 1937 was no exception.

During practically all of January, the polar front which ordinarily lies transverse to our coast line, was nearly parallel to it, conforming in this respect to the axis of the North Pacific high pressure area, which lay northwest to southeast most of the time. Hence, the frontal systems that formed or regenerated over the upper Gulf of Alaska, took a southerly course, each one bringing in its wake Polar Continental (*Pc*) air, which we are forced to conclude from the pilot balloon soundings over the region, came across the mountain ranges of Alaska and British Columbia—an extremely abnormal movement. As these disturbances moved southward they became the medium for the transport of air from the Polar Basin over our western states, giving them a distinctly continental rather than oceanic type of weather.

The outburst of January 18th resulted in the now historic cold wave. A *Pc* air mass with exceptionally low surface temperatures followed closely in the rear of a small depression, which, after its formation in the Gulf of Alaska, passed rapidly southward down the coast of British Columbia, and appeared over our Pacific Northwest on the 19th; Nevada and northern California on the 20th; and southern California and Arizona on the night of the 21st. Most of the Pacific and Plateau States at some time were under its domination, and minimum temperatures lower or closely approaching the record minimum were recorded at most of the stations in these districts."

MINIMUM TEMPERATURES IN THE DESERT

Figure 1 shows the minimum temperatures recorded in and near the Sonoran Desert during January, 1937. Very low temperatures occurred outside the desert on the high plateau of northern Arizona, -29°F. at Pine-dale being the coldest. From the northern section of the State there is a drop in altitude in general to the desert, where minimum temperatures ranged

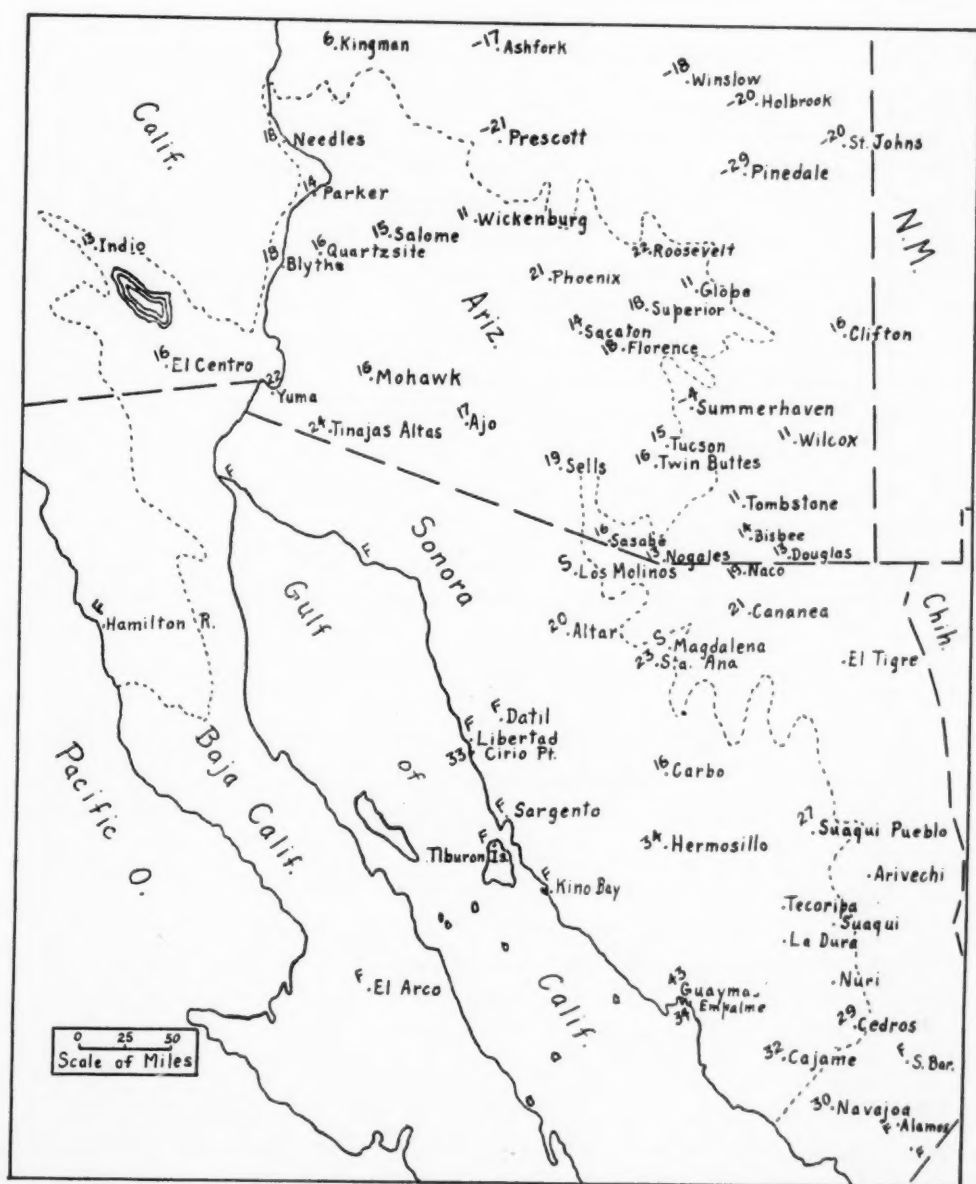


FIG. 1. Sonoran Desert Minimum Temperatures during cold wave of January, 1937. Temperatures are in degrees Fahrenheit, frost data alone denoted by *F*, dotted line represents Sonoran Desert Boundary, *S* denotes southern limit of snowfall in desert.

from 10 to 20°F. Such a marked difference in minimum temperatures between the two sections of Arizona cannot be explained on the basis of altitudinal considerations alone. Of course, the front portion of an invading cold air mass may be warmed sufficiently in its passage over the land to account for part of the discrepancy, only the front portion reaching the desert and the interior portion of the mass arriving in northern Arizona as cold air overlying an already cooled land surface. Furthermore, the moun-

tain chain separating the plateau of northern Arizona from the desert doubtless acts as a barrier which prevents the lowest, and potentially coldest, air from reaching the desert.

The fact that the desert stations are located quite at random with respect to topography prevents very detailed comparisons of these. However, the coldest desert temperatures occurred in the Arizona section near the northeast border of the Sonoran Desert. One very low reading in southern Arizona was -4° at Summerhaven, a mountain station at an elevation of 7,650 feet, actually above the desert in a coniferous forest. East of the Sonoran Desert the stations at Clifton, Willcox, Tombstone, Bisbee, Douglas, Nogales, Naco, and Cananea are at somewhat higher elevations than the desert stations, but their minimum readings were not appreciably colder. Stations in the state of Sonora did not experience weather as cold as those in Arizona, some actually having no frost. Along the coast of the Gulf of California frost was reported from several localities as far south as Kino Bay, but these were mild, as the 33° minimum at Cirio Point attests.

Light frost was reported at several localities in southern Sonora, the temperature falling to 30° at Navojoa. No frost has been reported from Sinaloa. In Baja California, Hamilton Ranch and El Arco Mine reported light frost.

Figure 2 is a minimum temperature map of the cold wave of January, 1913, the only cold spell on record more severe than the one of 1937. Arizona records only are presented here. In general, the desert stations reported temperatures several degrees colder in 1913 than in 1937. On the other hand the northern Arizona stations experienced colder weather in 1937, but unfortunately, too few stations are involved to lay much stress on these differences. A point of significance also is the fact that the 1937 cold wave lingered over an entire week while that of 1913 passed in three days.

Since ground inversions, which will be discussed later, were more strongly developed in 1913 (table 1), and since most of the stations are influenced by ground inversions, the general severity of the 1913 cold wave may not have been as pronounced as figure 2 indicates. It is highly probable, nevertheless, that the cold waves of 1913 and 1937 were very nearly the most severe ones that have been experienced by the flora of the Sonoran Desert as it is now constituted.

GROUND INVERSIONS

The Desert Laboratory stations are located on and near Tumamoc Hill, which rises 700 feet above the flood plain of the Santa Cruz River. The "hill" station of tables 1 and 2 is situated on the north slope of Tumamoc Hill, 330 feet above the plain from which the hill gradually rises; the "garden" station is on the level plain about 100 yards from the base of the hill. These two stations are one half mile apart, and are about 5 miles from the Tucson station. The data of tables 1 and 2 have been taken from thermo-

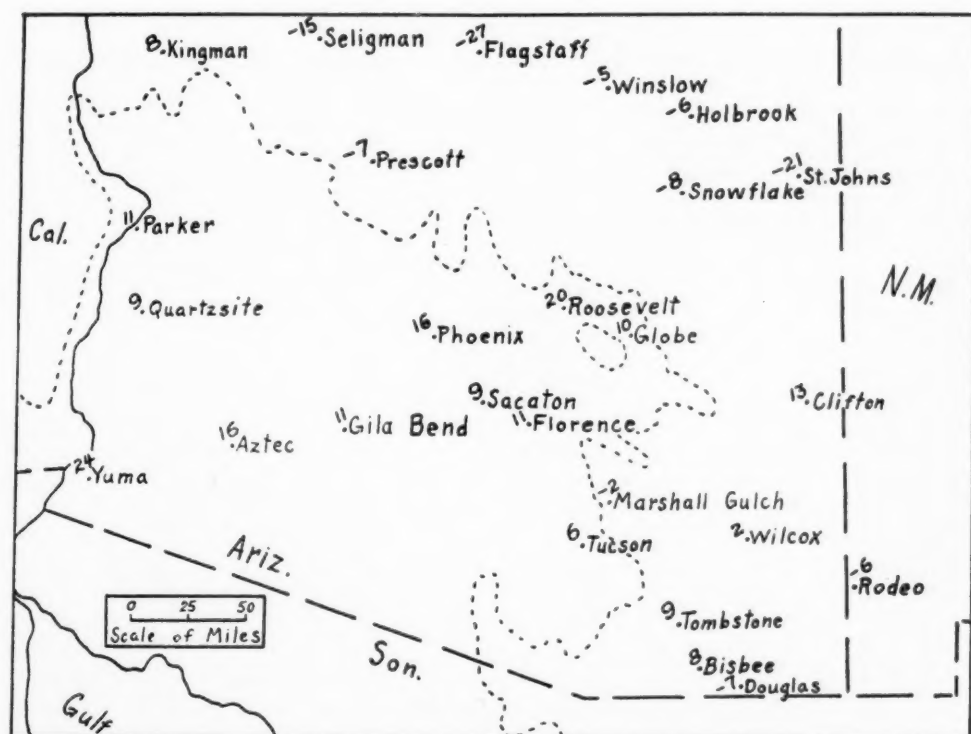


FIG. 2. Sonoran Desert Minimum Temperatures during cold wave of January, 1913. Temperatures are in degrees Fahrenheit, dotted line represents northern boundary of Sonoran Desert.

graph records which were obtained in standard Weather Bureau shelters 5 feet above the ground.

Nocturnal ground inversions of temperature are a common phenomenon in the Sonoran Desert. Young (1921) has studied them in the adjacent region of southern California. A ground inversion is an atmospheric condition in which the temperature increases with elevation from the ground, in basin localities, to as much as 1,000 feet in the air; above this zone a decrease of temperature with elevation exists. The frequency, intensity, and depth of inversions vary with different meteorological and topographic conditions. In earlier literature this phenomenon was called "cold air drainage," a term which infers more than the evidence justifies. These inversions are essentially layers of cold air which lie near the ground on calm, clear nights. They are highly local in character, develop only on nearly cloudless nights, require only a short time to form, are quickly destroyed (as layers with sharp vertical temperature gradients) by moderate wind movement, and vary in numerous details under different conditions of topography.

At the garden station ground inversions are often well developed and nearly of maximum intensity; the hill station is near the top of the inversion layer (Turnage, 1937). These facts explain the relatively low temperatures recorded at the garden station as shown in tables 1 and 2.

TABLE 1. MINIMUM TEMPERATURE DATA FOR "HILL" AND "GARDEN" STATIONS
NEAR TUCSON, ARIZONA

Winter	Minimum Temperature		Number of Freezing nights		Number of Freezing hours		Hour-degrees of Temperature below 32 F.	
	Hill	Garden	Hill	Garden	Hill	Garden	Hill	Garden
	Deg. F.	Deg. F.						
1912-13.....	15	1	9	..	81	..	480
1922-23.....	0	..	0	...	0
1923-24.....	0	..	0	...	0
1924-25.....	29	..	3	..	18	...	30
1925-26.....	0	..	0	...	0
1926-27.....	31	..	1	..	8	...	8
1927-28.....	31	..	2	..	15	...	15
1928-29.....	27	..	12	..	43	...	82
1929-30.....	31	..	1	..	6	...	6
1930-31.....	0	..	0	...	0
1931-32.....	20	..	18	..	103	...	367
1932-33.....	21	15	8	74	45	394	163	1808
1933-34.....	28	16	6	45	11	197	24	808
1934-35.....	21	12	5	36	35	227	130	1349
1935-36.....	30	19	4	54	5	253	7	1081
1936-37.....	16	11	15	54	123	336	588	1900

The hill station is perhaps more nearly representative of the general temperature conditions in the largest portion of the desert at elevations between 2,000 and 3,000 feet. The garden station more closely approximates conditions found in the basin areas, canyons and valleys.

Freezing weather in the Sonoran Desert is the result of either the development of a ground inversion at night (which affects only certain areas) or the influx of a cold northern air mass, or both these factors occurring simultaneously. Basins which experience well developed ground inversions are dependent in some measure upon the altitude of the basin; an inversion which would produce a few degrees of frost at Tucson might produce no frost at another basin station 1,000 feet lower under similar conditions.

Although a few inversions do occur which cause the minimum temperature at the garden to be more than 20° lower than that at the hill station, this is seldom the case during the coldest night of winter. The winter minimum usually occurs when a cold air mass has invaded the region as a consequence of the passage of a cyclone. The meteorological conditions of the storm are such as to inhibit the maximum development of an inversion. The minimum temperatures of the 1936-37 winter illustrate the influence of storm conditions at the time of coldest weather when the garden was only 5° colder than the hill station (Fig. 4). The 1912-13 winter minimum occurred on a more calm night, and the difference between the two stations was 14°F.

TABLE 2. GREATEST NUMBER OF CONSECUTIVE HOURS AND OF HOUR-DEGREES BELOW 32°F., DATES OF FIRST AND LAST FREEZES, AND LENGTH OF FREEZE SEASON AT "HILL" AND "GARDEN" STATIONS NEAR TUCSON, ARIZONA

Winter	Greatest number of consecutive hours below 32 F.		Greatest number of consecutive hour-degrees below 32 F.		Dates of first and last freezes		Length of freeze season (days)	
	Hill	Garden	Hill	Garden	Hill	Garden	Hill	Garden
1912-13.....	19	..	214	...	{ Jan. 6 } { Mar. 31 }	84	...
1922-23.....	0	..	0	0	...
1923-24.....	0	..	0	0	...
1924-25.....	8	..	17	...	{ Jan. 13 } { Jan. 18 }	6	...
1925-26.....	0	..	0	0	...
1926-27.....	8	..	8	...	Dec. 28	1	...
1927-28.....	9	..	9	...	{ Feb. 16 } { Feb. 17 }	2	...
1928-29.....	11	..	37	...	{ Dec. 11 } { Feb. 27 }	78	...
1929-30.....	6	..	6	...	Jan. 9	1	...
1930-31.....	0	..	0	0	...
1931-32.....	15	..	85	...	{ Dec. 15 } { Feb. 4 }	51	...
1932-33.....	14	15	90	148	{ Dec. 26 } { Feb. 11 }	{ Nov. 10 } { Apr. 20 }	47	161
1933-34.....	5	12	14	106	{ Dec. 17 } { Jan. 14 }	{ Nov. 5 } { Apr. 4 }	28	150
1934-35.....	16	17	95	136	{ Jan. 20 } { Mar. 10 }	{ Nov. 21 } { Apr. 10 }	49	140
1935-36.....	2	10	3	86	{ Jan. 2 } { Jan. 20 }	{ Oct. 24 } { Apr. 6 }	19	164
1936-37.....	19	17	185	193	{ Jan. 3 } { Feb. 9 }	{ Nov. 3 } { Apr. 24 }	37	172

The ground inversion is also responsible for considerably more freezing nights in the garden than on the hill. In the winter of 1931-32 there were 18 freezing nights on the hill, but no freezing temperatures were recorded in four of the winters shown in table 2. At the garden there have been from 36 to 74 freezing nights each winter. The garden is also subjected to freezing weather considerably earlier in the fall and later in the spring than is the hill station. During the periods covered by these records—15 consecutive years at the hill and 5 consecutive years at the garden—the earliest freeze at the former station occurred December 11 and at the latter October 24; the latest freeze of spring at the former station occurred March 31 and at the latter April 24. The very early and very late occurrences of frost at the garden extend well into the growing season and exert a deterrent effect on vegetative activity.

The combination of many more freezing nights and of appreciably lower temperatures at the base of the inversion is responsible for the markedly greater number of "hour-degrees" of freezing weather in the garden. This

datum is an attempt to coordinate the influences of intensity and of duration of freezing weather somewhat along the lines suggested by MacDougal (1914). Seasonal totals range from 808 to 1,900 hour-degrees at the garden and from 0 to 588 at the hill. More significant than seasonal totals, as far as frost damage to established plants is concerned, is the number of consecutive hour-degrees of freezing weather. In only one year of five has the greatest number of consecutive hour-degrees fallen below 100 in the garden; only in one year of the last 15 has it risen above 100 on the hill.

The fact that during the one very cold night (January 22, 1937) of nearly a quarter of a century the cold conditions were such that the garden and hill endured approximately the same number of hour-degrees—193 and 185 respectively—appears to be important. The freeze of January 7, 1913, with 214 hour-degrees on the hill, was slightly more severe, and indicates further that occasional freezes above the body of air subject to the development of a ground inversion are as severe as those within an inversion layer. Furthermore, table 1 reveals that the year to year variation in severity, as measured by hour-degrees, is much greater on the hill than in the garden.

A ground inversion freeze which falls to a given minimum temperature produces appreciably fewer hour-degrees than does a purely cold-air-mass freeze. For instance, the coldest night of the 1933-34 winter, a ground inversion phenomenon largely, reached 16° and produced 106 hour-degrees below 32° at the garden. The 16° minimum at the hill in the winter of 1936-37, a cold wave, produced 185 hour-degrees. Although cooling is rapid at the base of the inversion layer after sundown, the general heat conditions of the entire air mass are usually such that the duration of the freeze is limited. In the cases cited the inversion freeze lasted 12 hours while that of the cold wave lasted 19 hours.

ANOTHER THIN INVERSION LAYER

There is another fact of significance concerning inversions which is not shown by the ordinary records. During inversion nights a very thin layer (several inches) of cold air lies next to the ground of hill slopes. This layer is to be distinguished from the main inversion layer in that it is much thinner, has a very steep temperature gradient, is not found at all spots on the slope, and may or may not lie within the larger inversion layer. An alcohol minimum thermometer was exposed openly one inch above the ground at the hill station. The minimum temperature record thus obtained compared very closely with that of the garden thermograph (5 feet above the ground and in a shelter). Numerous checks with thermocouples and mercurial thermometers, variously painted and variously shielded, indicated that the error due to open exposure of the alcohol thermometer was of slight significance as far as the present inference is concerned. Likewise, readings were obtained in the patio of the nearby Laboratory building. These revealed no marked difference between the surface air layer in the patio and the 5-foot layer of the hill temperature station.

Hence there are certain spots on hill slopes where the cold conditions of a thin layer of air are very similar to the conditions of larger layers in the basins. Minimum temperatures, length of the frost season, and number of freezing nights are closely parallel, judging from the meagre data available. This thin layer of cold air on the hill slopes, while of little moment to the larger plants, is a strong force with which all seedlings must contend. There are many spots which, like the Laboratory patio, do not have this thin, cold layer, no doubt, but the authors' experience indicates these to be the exception rather than the rule.

DURATION OF FREEZE OF PARAMOUNT IMPORTANCE

As Shreve (1911, 1914) has demonstrated, the number of consecutive hours of freezing weather is a cold temperature datum of paramount importance in this region. Figure 3, by Shreve, presents isochronals for the longest number of consecutive hours of freezing temperature at selected stations. In the Sonoran Desert there is no record of a single day (between two cold nights) when the air temperature failed to rise above 32° . At Tucson there have been two occasions of 19 consecutive freezing hours (table 2). These occurred on the hill; the longest freeze at the garden was 17 hours. The lowest maximum daytime air temperature record at the hill station was 35° —January 7, 1913—with 15 hour-degrees above freezing and 6 hours above freezing during the day, preceded by 19 hours and followed by 15 hours below freezing. The second lowest maximum, 36° , occurred January 22, 1937; there were only 5 hour-degrees above freezing and 2 hours

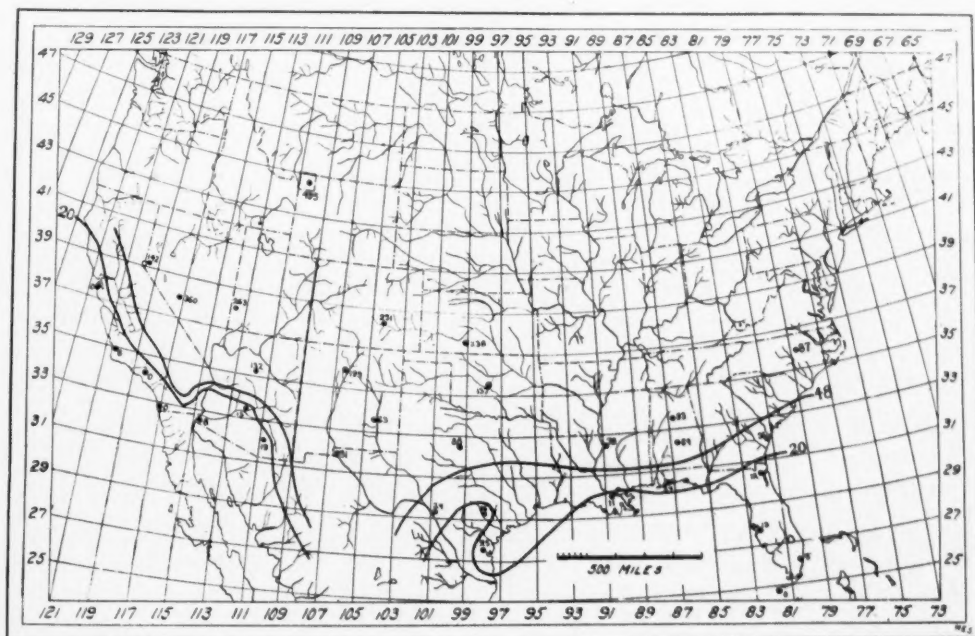


FIG. 3. Isochronals for longest number of consecutive hours of freezing temperature, 1917-20. (After Shreve.)

above freezing during the day, also preceded by 19 hours and followed by 15 hours below freezing.

This short duration of freeze contrasts sharply with that found in northern Arizona where there are often 5 consecutive days and nights of continuously freezing air temperatures. Although minimum temperatures are very little lower in the region east of the Sonoran Desert than are the desert temperatures, as figures 1 and 2 show, the duration of freezing weather is probably considerably longer. This is evidenced by the Bisbee record of January 7, 1913, when the maximum daytime air temperature failed to rise above 24° . The freezing weather at Bisbee on that date lasted at least 36 consecutive hours or nearly double the duration of Sonoran Desert freezes. The higher mountain peaks in, or rather above, the desert also have freezing weather which extends over a period of several days and nights, as shown by the Santa Catalina record to be discussed later.

Figure 4 shows thermograph traces of the January, 1937, cold wave which invaded the region as a cyclonic storm; the broken line is the hill station and the unbroken line is the garden station record. During the first two nights, with storm conditions prevalent, no inversion developed. The third night, January 22, which was the coldest night, only a slight inversion developed. The following nights, after the storm center had passed, inversions were somewhat more pronounced, but the air mass was not as cold as in the earlier stages. The record for March 2, 1937 (Fig. 4) illustrates the nature of the temperature curves when an inversion is fairly well developed. It further illustrates the occurrence of freezing weather in the garden on nights when the air mass is in general fairly warm and temperatures at the hill station are mild.

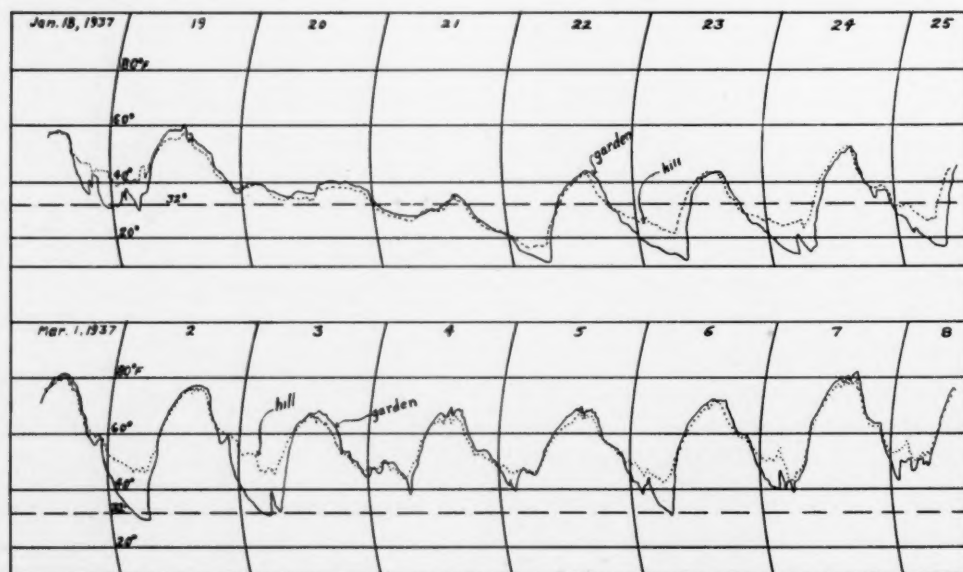


FIG. 4. Thermograph records from garden and hill stations, Desert Laboratory, for the January, 1937, cold spell and for week ending March 8, 1937, a typical winter season week.

The temperature of the soil is also a datum of some value in this connection. The only instrument from which we have a soil temperature record is a Freiz soil thermograph with bulb buried as shallowly as possible in the adobe soil of the garden station. The maximum soil temperature of January 21, 1937, was 41°F. followed by a minimum of 18°. For 18 consecutive hours the temperature was below 32° and there were 161 hour-degrees below 32°. During the next 3 days and nights the soil was only slightly warmer, fluctuating diurnally between about 50° and 20°. This soil, quite moist, froze to a depth of 3 inches. Rains and snows earlier in the month, amounting to 1.50 inches of precipitation, had left the first 10 inches of soil very moist. In shady spots on the north slope of Tumamoc Hill snow remained on the ground for one week, although in most places it had melted after a few hours of sunshine.

Wind velocities at Tucson during the snow storm preceding the coldest weather were rather high, approximately 10 miles per hour. During the coldest period the air was relatively calm, from 3 to 7 miles per hour.

MOUNTAINS OVERLOOKING THE DESERT

The pine-clad Santa Catalina Mountains stand on the eastern edge of the Sonoran Desert, a few miles north of Tucson, and rise to an elevation of 9,150 feet. Minimum temperature readings at several stations on the Santa Catalina slopes were reported by Shreve (1914) for the winter of 1912-13. During that severe winter the garden station, at the base of an inversion, recorded 1°; the coldest reading, -6°, occurred at an altitude of 6,000 feet on a ridge; in a canyon at 7,700 feet the minimum temperature was -2°.

Daily readings were made by Mr. R. B. O'Neill throughout the 1933-34 winter at Summerhaven, altitude 7,600 feet, in a canyon of the Santa Catalinas. This was a rather mild winter and the coldest temperature at Summerhaven was 17° as compared with 16° at the garden and 28° at the hill station. Again daily readings were made at Summerhaven throughout the severe 1936-37 winter. The minimum at Summerhaven of -4° compares with 11° at the garden and 16° at the hill.

These data indicate that the high mountains of southern Arizona do not experience minimum temperatures very much colder than are those of the desert lowlands, and not nearly as cold as stations at comparable elevations on the plateau of northern Arizona.

The Summerhaven station from November 25, 1933, until the summer of 1934 had 57 nights of temperature below 32°. The garden station over the same period had 39; the hill had only 6 nights. From December 7, 1936, until the summer of 1937 the Summerhaven station experienced 103 nights below 32°, the garden 51, and the hill 15 nights. The last 32° minimum of the 1934 spring occurred at Summerhaven April 7, at the garden April 4, and at the hill January 14. In 1937 the last 32° minimum of spring occurred at Summerhaven May 1, at the garden April 24, and at the hill February 9.

It has long been suspected that the most potent cold temperature factor on the high mountain slopes of southern Arizona, in so far as the absence of desert plants is concerned, is the duration of the freezing spells. Mr. O'Neill's Summerhaven records lend considerable weight to this hypothesis. In the 1933-34 winter there were two consecutive days in which the maximum temperature reached only 28° and 30° respectively, during a prolonged snow storm. The duration of that freeze was about 60 hours. There were two other occasions when single days were without thaw. One of these experienced snow; the other came several days after a storm.

The January, 1937, cold wave produced maximum temperatures at Summerhaven of 32°, 26°, 22°, 32°, and 26° for 5 consecutive days. This was a period of about 130 consecutive hours without thaw, which is closely comparable to freeze durations in northern Arizona. Earlier in the winter there was a period of 4 consecutive days without thaw, another of 3; later there were periods of 1 day and of 2 days. All of these periods except the one of a single day occurred in conjunction with snow storms.

There is a need for thermograph records from stations on the desert boundary in order to determine more accurately the cold temperature features which correlate with the change in vegetation. The northward and vertical limits of desert vegetation in Arizona appear to be determined by the fact that the duration of occasional freezes beyond these boundaries amounts to from 36 to 130 hours, but further detailed evidence is needed.

YAQUI RIVER RECORDS

In table 3 are given the annual minimum temperature records of the periods 1927 through 1930 and 1933 through 1936 from several stations on the Yaqui River of Sonora and Chihuahua. These data were kindly supplied by the Richardson Construction Company of Cajeme, Sonora. Figure 1 shows the location of several of the stations. Madera and Dolores are just off the map in Chihuahua east of Arivechi. At the desert stations of Suaqui, La Dura, Tecoripa, San Xavier, and Nuri only two occasions of mild freeze were noted for the periods covered. At Arivechi and Dolores,

TABLE 3. MINIMUM TEMPERATURES ALONG THE RIO YAQUI¹

	Elevation	1927	1928	1929	1930	1933	1934	1935	1936
La Dura, Son.....	500 ft.	49°F.	43.0	46.5	44.5	46.5	35.5	41.0	37.6
Nuri, ".....	1,000	48.0	46.5	35.5	48.0	44.5	35.5	35.5	34.0
Tecoripa, ".....	1,000	39.0	32.0	34.0	39.0	41.0	37.5	32.0	35.5
Arivechi, ".....	2,000	14.0?	12.0?	14.0?	12.0?	35.6	30.0	26.5	34.0
Suaqui, ".....	1,300	41.0	37.5	39.0	39.0	43.0	32.0	17.5?	35.5
San Xavier, ".....	43.0	41.0	39.0	39.0	46.5	43.0	41.0	41.0
El Tigre, ".....	4,000	28.5	21.0	25.0	25.0	19.5	30.0	17.5	28.5
Dolores, Chih.....	3,700	34.0	32.0	32.0	5.0?	34.0	34.0	32.0	34.0
Madera, ".....	7,000	12.0	10.5	8.5	7.0	16.0	16.0	17.5	16.0

¹ A question mark (?) is placed after the readings which appear to be in error with respect to a comparison of the mean monthly minimum records for these stations for the different years.

just east of the southern part of the Sonoran Desert, freezes are more common but also mild. El Tigre is visited by cold every year, and probably has a weather regime similar to that at Douglas and Bisbee. Madera, high in the heart of the Sierra Madre, is visited by freezes every year, the lowest minimum noted in these data being 7°. In the Sierra Madre the duration of freeze is not known from available records. It is possible that the eastern edge of the desert, against the slopes of the Sierra Madre, is determined by factors other than cold weather.

INFLUENCE EXERTED ON VEGETATION BY COLD WAVE OF JANUARY, 1937

The desert merges gradually into thorn forest in southern Sonora. In this transition region there is a profound change in plant life (Shreve, 1934) which correlates with the southern extension of freezing weather (excepting in the mountain areas). Undoubtedly many of the species of the south are unable to endure frost, although there are probably many other species for which frost is not a critical condition in checking their northward extension. Distributional evidence indicates that the thorn forest has contributed heavily to the Sonoran desert flora, and the inference is strong that this contribution is still going on—that many species here will continue to migrate slowly northward.

The data on frost damage are presented in geographical order beginning with the southern edge of the desert and working northward.

SOUTHERN SONORA

Our sincere thanks are due Mr. Howard Scott Gentry for the full use of his notes on the plants of southern Sonora. The coldest temperature recorded was 29°F. at Cedros with 5 nights of frost.

Among the species injured are:

I. Species with northern limit in southern Sonora

A. Leaves and branches damaged

Ficus, several species, including *F. cotinifolia* and *F. petiolaris*
Pithecolobium dulce
Randia echinocarpa
Perityle cordifolia
Mammillaria sp. crown damaged in several species
Tournefortia Hartwegiana

B. Leaves damaged

Albizia tomentosa
Quercus albocincta
Ichthyomethia mollis

- C. Flowers damaged
Brongniartia lunata
- II. Species with northern limit in central Sonora
 - A. Leaves and branches damaged
Guazuma ulmifolia
Caesalpinia pulcherrima
 - B. Leaves damaged
Lysiloma Watsoni
Randia obcordata
Jacquinia pungens
Stegnosperma halimifolium
 - C. Flowers damaged
Ipomoea arborescens
- III. Species with northern limit near northern boundary of Sonoran Desert
 - A. Leaves and branches damaged
Franseria ambrosioides
 - B. Leaves damaged
Sapindus Saponaria
 - C. Flowers damaged
Asclepias subulata

Cultivated plants damaged and in some cases killed in southern Sonora include *Citrus spinosissima*, *Carica papaya*, *Musa sapientum*, and *Ricinus communis*.

Pentstemon Parryi, which has its southern limit in this region, suffered frosted flowers.

SASABE TO ALTAR AND TIBURON ISLAND

Late in April, 1937, one of the authors journeyed from Tucson to Tiburon Island via Sasabe, Altar, Datil, Libertad, and Sargento. Although frost damage was more difficult to discern at that late date, some damage was nevertheless apparent. Figure 1 shows the minimum temperatures along this route.

Leaves and twigs of *Celtis pallida* and *Olneya Tesota* were injured as far south as the vicinity of Datil. Tips of branches of *Lophocereus Schottii* were frosted on occasional plants in some localities from Altar to Datil. Leaves and shoots of *Bursera microphylla* were damaged at every locality excepting the interior of Tiburon Island, and the leaves were killed on plants near the Cirio Point station, where the minimum temperature was only 33°. No damage was noted on *Pachycereus Pringlei*. Judging from the appearance of the plants, the Datil area had received more cold weather than any other locality south of the border along this route.

PAPAGO RESERVATION

The authors owe their thanks to Dr. R. R. Humphrey, who spent the 1936-37 winter on the Papago Reservation between Sells and Ajo, for the use of his observations on frost damage. Here leaves and stems were damaged on *Olneya Tesota*, *Bursera microphylla*, *Jatropha cardiophylla*, *Encelia farinosa*, and *Sapium biloculare*. Tips of *Lemaireocereus Thurberi* were injured.

Just south of Ajo is the northern limit of *L. Thurberi* excepting the occurrence of a single large individual on a slope of the Picacho Mountains about 40 miles northwest of Tucson. This unique individual was not damaged by the cold weather, due partly to its location with respect to surrounding topography where it escapes the nocturnal inversions of temperature. Although the tips of the plants near Ajo were killed, growth has resumed without the loss of many if any individuals.

TUCSON REGION

Among the native species leaves and twigs of *Olneya Tesota* and *Celtis pallida* were killed. In many cases stems were killed to the ground in *Franseria ambrosioides*, *Jatropha cardiophylla*, and *Encelia farinosa*. Frosted leaves were noted on *Dodonaea viscosa* growing in the arroyo bottoms.

Several individuals of *Lophocereus Schottii*, *Lemaireocereus Thurberi*, and *Rathbunia alamosensis*, which had been imported from Sonora several years ago and planted at the Desert Laboratory, suffered dead tips, but all these plants have resumed growth. *Ceiba acuminata*, imported from Sonora, suffered death to stems at Tucson but later sent up new shoots. Seedlings of *Zizyphus sonorensis* and *Pithecolobium sonorae* were killed at the Desert Laboratory Garden. One young *Jatropha cordata* was killed, another has recovered.

Of the *Opuntias* no record was kept concerning frost damage. Exotic plants in the Laboratory greenhouse, as well as native seedlings, were unhurt, as the greenhouse had been heated in anticipation of the cold wave. Palm and citrus trees around Tucson suffered varying degrees of injury. Old leaves of *Prosopis velutina* Wooton were shed during the cold spell, but this may have been due largely to the snowfall. Leaves of *Cercidium Torreyanum* and *C. microphyllum* were killed. *Idria columnaris*, from Sonora, was not injured at Tucson.

In January *Fouquieria splendens* was not in leaf. However, the young leaves of one individual at the garden were killed by the frost of February 21, 1937. This inversion type of cold weather produced 8 hours of frost, 58 hour-degrees below 32°, and a minimum temperature of 21°. A month later new leaves had come out again on this individual.

SUPERIOR REGION

Mr. Jack Whitehead, to whom the authors are deeply indebted for his contribution, observed the frost damage to native species in the vicinity of

Superior, and also listed the damage done to the many exotic plants of the Boyce Thompson Arboretum.² The cold conditions at Superior were comparable to those at Tucson, the minimum temperature being somewhat higher, however (see figure 1).

Around Superior damage to leaves and stems was suffered by *Olneya Tesota*, *Celtis pallida*, *Asclepias subulata*, *Encelia farinosa*, *Dodonaea viscosa*, and *Simmondsia californica*. The last two species were in flower at the time of the freeze, the flowers being killed. As a result the 1937 seed crop of *S. californica* was extremely meagre. Frost damage to all these plants was variable from one locality to another, some stands of *Olneya Tesota* and *Dodonaea viscosa* showing little or no injury. *Franseria ambrosioides* stems were killed to the ground. With the advent of the growing season all these species resumed growth.

Among the species cultivated in the Arboretum grounds *Lysiloma Thunbergii*, native to the Rincon Mountains near Tucson, suffered considerable damage but recovered. Among plants more or less severely injured were: *Randia Thunbergii*, *Duranta Plumieri*, *Karwinskia Humboldtiana*, *Lantana Camara*, *Tecoma stans*, and *Fouquieria peninsularis*, all of which are native to the southern portion of the Sonoran Desert in Sonora or Baja California.

Some damage to cacti—*Lemaireocereus Thunbergii*, *Opuntia Bigelovii*, *Opuntia fulgida mammillata*, and *Opuntia leptocaulis*—occurred at the Arboretum. Cacti badly damaged included *Lophocereus Schottii*, *Pachycereus Pringlei*, *Rathbunia alamosensis*, *Mammillaria microcarpa* and *M. Milleri*. The last two showed death of many individuals, which is surprising in view of the fact that the range of these species is roughly from Kingman to Phoenix near the northern boundary of the desert.

NORTHERN PART OF SONORAN DESERT

After the cold wave Dr. Shreve noted dead twigs and foliage of *Olneya Tesota* at its northern limit immediately north of the Bill Williams River; the same condition prevailed in the *Olneya* region of southern California. *Franseria ambrosioides* throughout the Bill Williams Valley at its northern limit was killed to the ground. Leaves and branches of *Eucnide urens* were frost damaged. *Encelia farinosa* growing in the lower spots of the Bill Williams region was damaged, but little injury was observed to those plants growing somewhat higher on the slopes, presumably above a ground temperature inversion. In the Tucson Mountains at its northernmost locality *Eysenhardtia orthocarpa*, observed in late summer, appeared to have been frosted to the ground, but new shoots were abundant.

SOUTHERN UTAH

In the vicinity of St. George, Utah, several Sonoran desert species reach their northern limit. Cottam (1937) has reported severe damage to *Covillea*

² This list of exotic plants which were damaged will be supplied by the authors to any reader who wishes it.

tridentata (*Larrea tridentata*), *Strombocarpa odorata* (*Prosopis pubescens*), and *Prosopis glandulosa*. Dr. Cottam has recently informed us that all these species are recovering, new growth from primary branches being abundant, but that at the higher elevations the mortality to *Larrea* and *Prosopis glandulosa* was as high as 80 per cent of the individuals. The freeze, which was the most severe on the St. George records, produced 7 consecutive days of weather below 32° and a minimum temperature of -11°.

BAJA CALIFORNIA

From Baja California we are informed by Mr. L. L. Logan that occasional banana trees were injured at Hamilton ranch. Mr. James Harding reports frost damaged leaves to "torote" (probably *Pachycormus discolor*).

DISCUSSION

The cold wave of January, 1937, was in many respects the most severe freeze that has invaded the Sonoran Desert during the period covered by climatic records. The influence of this freeze on the various species of plants affords some indication of the role of freezing weather in determining the distribution of the desert flora. Conclusions, however, owing to the complexity of this problem must be drawn with care.

The entire area of the Sonoran Desert is subject to occasional frosts. The low country bordering the Gulf of California, southern Sonora, and the desert of Baja California experience less cold weather than do other parts of the desert. The coldest weather is experienced by the northern fringe of the desert in Arizona and by the plains at higher altitudes.

Topographic location contributes to extreme variability in the incidence of freezing weather, stations situated within the ground inversion zone receiving considerably more cold air than others. However, occasional cold waves, often occurring only once in several years, produce the extreme freezes at all stations, and cause the most damage to plants.

Two features of cold temperature stand out above others. The first is the occurrence of frost; the second is the duration of freezing temperatures throughout a night, the following day and the following night, and even longer perhaps. The southward limit of this first cold weather datum coincides roughly with the northward extension of the tropical thorn forest (southern limit of the desert). The second datum coincides with the northern limit of the Sonoran Desert and with the vertical limit of desert vegetation on mountain slopes and tablelands. Although the most profound changes in vegetation occur at these boundaries, there are many species which have their distributional limits somewhere between them.

For certain of the latter group of species, no doubt, there are intermediate cold temperature features made up of both intensity and duration which are critical. We do not yet have definite evidence as to the quantities.

A few species extend beyond the Sonoran Desert. *Larrea tridentata* has endured at St. George, Utah, a period colder than any occurring on the high mountain slopes within and bordering the desert, on which this species is not found. *Fouquieria splendens* grows beyond the desert in regions where the duration of a freeze is more than 36 hours.

The northwestern boundary of the Sonoran Desert in California, where the Sonoran and Mohave Deserts meet, does not correlate with the cold temperature features we have discussed. The absence of characteristic Sonoran species in the Mohave Desert is thought to be related to the absence of summer rainfall.

With the exceptions of *Prosopis glandulosa* and *Larrea tridentata* at some localities near St. George, Utah, we have no evidence that wholesale killing of any species has occurred along its northern, or cold, limit. The fact that injury to *Franseria ambrosioides*, for instance, was almost as severe in southern Sonora as in the Bill Williams region indicates that partial killing of a plant is not an infallible index that the critical cold temperature has been approached.

Nevertheless, it is highly probable that those species which experienced damage are hindered by cold weather from migrating much farther into colder regions. Among these species, which extend to the northern boundary of the desert, are *Olneya Tesota*, *Franseria ambrosioides*, *Encelia farinosa*, *Simmondsia californica*, *Celtis pallida*, *Mammillaria microcarpa*, and *M. Milleri*.

Although no damage to *Carnegiea gigantea* was noted, it has probably migrated as far north as cold weather will allow (Shreve 1911). In fact, in the 1913 cold wave Thornber (1916) reported death to young *Carnegieas* growing near their altitudinal limits. There are many species, no doubt, which suffered no damage in the recent freeze but are unable to endure the long duration of cold weather characteristic of the region north of the desert.

Among the species which have their northern limit near a line between Yuma and Superior those which were frost damaged include *Bursera microphylla*, *Lemaireocereus Thurberi*, *Dodonaea viscosa*, *Asclepias subulata*, *Sapium biloculare*, *Jatropha cardiophylla*, *Lysiloma Thornberi*, and *Eysenhardtia orthocarpa*. The Desert Laboratory record of a minimum temperature of 16°F., 19 consecutive hours of freezing weather, and 185 consecutive hour-degrees below 32° is some index of the critical cold for these species. A minimum temperature near 0°F., 20 consecutive hours and about 250 hour-degrees below 32° is probably a fair index of the critical cold endured by the species which suffered along the northern border of the desert.

Among the Sonoran Desert species which do not extend into Arizona those which suffered frost injury at Superior or Tucson (in cultivation) included *Pachycereus Pringlei*, *Lophocereus Schottii*, *Rathbunia alamosensis*,

seedlings of *Zizyphus sonorensis* and *Pithecolobium dulce*, *Jatropha cordata*, *Randia Thurberi*, *Duranta Plumieri*, *Karwinskia Humboldtiana*, *Lantana Camara*, *Fouquieria peninsularis*, and *Tecoma stans*. Few of these, however, were completely killed.

Mild frost in Baja California damaged *Pachycormus discolor*. The injured plants of southern Sonora, where frost was not extreme, have already been listed in the order of their distributional limits. Several of these species, although injured by mild frost in southern Sonora, extend into the central part of the state where freezes were somewhat more severe.

Of considerable interest is *Idria columnaris*, which was unhurt by Tucson's freeze, although its native habitat is in the relatively mild regions to the south.

Since our information concerning the various aspects of cold weather is limited at the present time, an imperfect picture of frost conditions in the Sonoran Desert is presented. The thin layer of cold air near the ground, presumably at most topographic sites on inversion nights, is probably a potent factor in a seedling's struggle for establishment. We know very little as yet about this air layer. Also, available temperature records seldom reveal information concerning duration of frost. Very few records exist of soil temperatures and the duration and depth of soil freeze. Most observers are still content with a record of daily maximum and minimum air temperatures obtained at an arbitrary height and place and of relatively insignificant "mean" figures. Very few attempts have been made to determine experimentally the critical temperature features for various plants.

Distribution of species under present climatic conditions surely has not reached a static state. Perhaps the northern limit of many Sonoran Desert species might be determined by factors other than winter cold, for instance, moisture relations. Accessory physical conditions might greatly modify the influence of cold weather—to such an extent that a single datum of freeze is a poor index of the limiting factors when applied to different localities and at different times for the same species. These are problems for the future.

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THE RELATIONS OF TEXAS ACRIDIDAE
TO PLANTS AND SOILS

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THE RELATIONS OF TEXAS ACRIDIDAE TO PLANTS AND SOILS

INTRODUCTION¹

Grasshoppers and war have come down through the ages as an ever-present twin menace to the amplitude of man's bread basket.

Grasshoppers, at least, have proved useful as well as destructive. The accumulation of three decades of significant cytological and genetical researches by McClung, Nabours, their colleagues and students has focussed the attention of biologists on the Acrididae as suitable material for the investigation of fundamental problems of biology. *Melanoplus differentialis* (Thos.) in the laboratories of McClung and Bodine has come to be recognized as a standard laboratory animal (Hodge 1933, p. 306), useful in the study of morphological, physiological, embryological and related problems. Furthermore, in addition to their taxonomic, evolutionary, and economic importance, animal ecologists have been looking to acridians as promising material which may afford some clues as to the relative individual values of the intricate complex of ecological factors which are involved in the interrelationship of terrestrial biota.

THE PROBLEM STATED

What are the factors that influence and control local distribution of the Acrididae? Is local distribution of grasshoppers chiefly correlated with the distribution of host-plants, with the food and protection afforded by the vegetation? How do different kinds of soils, soil texture, soil structure, soil moisture, chemical make-up of soils affect local distribution? To what extent do general climatic conditions, temperature, sunlight, humidity, and evaporation control distribution?

In some instances local distribution takes on the aspect of definite zonation and has been described as zonal distribution. In other areas zones are not apparent and a field study station is best described as a complex of intermingled habitats.

What is the relative importance of these environmental factors? To get an answer or a partial answer to this query has been the focus of a continuous series of field and experimental studies by the writer for the past seven years. Based on these researches, begun with field studies in 1931, an effort is being made in the present paper to analyze especially the plant and soil interrelationships of north central Texas acridians; and further to

¹ During 1935 and 1936 the writer was assisted in these investigations by grants-in-aid from the National Research Council. The 1937 experiments were supported in part by a grant from the Penrose Fund of the American Philosophical Society.

make a contribution to the understanding of the terrestrial biota as it is found in *north central* Texas.²

The statement of the Entomological Commission (Riley, Packard, and Thomas 1877, p. 13) applied to the "Rocky Mountain locust," *Melanoplus spretus* Walsh, as "devouring everything green" has been carried over generally by authors in describing the feeding behavior of grasshoppers.

Economic entomologists in describing the feeding activities of grasshoppers as a rule do not discriminate between "pest" species and those species which have not, as yet, been proven harmful to agriculture. The implication always is that all acridian species are potential enemies of cultivated crops. The following citations are typical. Essig (1926, p. 72) describes grasshoppers as "omnivorous feeders"; Herrick (1925, p. 328) as "destroying everything in their path"; Fernald (1921, p. 82) as "feeders on grasses and vegetation in general." Criddle (1933a, p. 478) is more critical in his observations. He points out that even *Camnula pellucida* Sc., a serious grasshopper pest, is a restricted feeder, and in cage tests he has shown that many Manitoba acridians are selective feeders.

Among recent ecological investigators, Wolcott (1936, pp. 79, 81) states that grasshoppers "like cows feed on any kind of vegetation," and Strohecker (1937, p. 245) says that "such plants as can be used for one species are equally useful for others." On the other hand, Ball (1936, p. 680), chiefly on the basis of his field studies, emphasizes "the diversity of adaptation and at the same time the fixity of these food habits."

In a recent paper (Isely 1937, p. 325) I have emphasized the importance of soils in explaining the local distribution of acridians. The further discussion of relations of the Acrididae to soils in the present paper is based in part on experimental data. These were secured by testing acridian reactions in choosing soils of different structure and texture for oviposition. Additional field data based on further critical studies of hatching sites are also discussed.

Experimental testing of acridian plant preferences for food, and soil choices for oviposition, was begun in 1935 and continued during 1936. Re-checkings and additional studies were made in 1937.

Topography and vegetation as related to drainage and shelter are important factors of the environment. Preliminary experiments dealing with variation in temperature and humidity correlate with field data in pointing to vegetation-cover for shelter as an important factor which must be further evaluated in explaining local acridian distribution. The habitat factors covering distribution in various micro-habitats as well as eco-climates³ and micro-climates have not been experimentally studied. Only general climatological conditions are, here, taken into account.

² In previous papers by the writer (1935, 1937) the acridian species studied came from widely separated stations in northeastern Texas. The experimental species which have supplied the data for this paper belong primarily to a more limited area geographically. Hence, the limitation, *north central* Texas.

³ The sum-total of meteorological factors within a habitat (Uvarov 1931, p. 128).

In attempting an analysis of certain factors that control local distribution, it may be well to define the scope of the distribution implied. Local distribution as here used means distribution within a limited area, an area which can be given a comprehensive examination in two or three hours' time by an experienced field worker. For a final thorough evaluation of the factors controlling local distribution from the viewpoint of field ecology, the same series of habitats of a given field-station should be examined at least bi-monthly so as to make sure of seasonal succession. For an understanding of annual fluctuations several years of continuous study would give more complete data. Diurnal and weather variations should not be overlooked in planning field study trips.

A field station should represent a specific type of habitat. The topography should be essentially uniform and the vegetation-cover similar as to plant species and density of cover. The area should be large enough (ten to twenty acres) to insure permanence of typical species even in unfavorable seasons. Marginal areas should be available for comparison. Possibly a better picture of what I mean by a limited area may be indicated by describing specific areas or local field-stations; for example: a sandy east Texas post oak cross-timbers tract including timber margins; a Houston clay shallow phase, upland, weedy pasture; a Houston black clay, level meadow; an eroded chalk or marl tract of rough, waste-land with sparse cover of mixed vegetation; an alluvial Trinity clay, creek valley, weedy-pasture including stream margins.

These general habitat types are represented at field-stations in Ellis, Dallas, and Johnson counties in north central Texas. These areas have essentially uniform⁴ general climatological influences. Such climatological factors have been determined by making use of the United States weather records: temperature, precipitation, pressure, wind, sunshine, and in some instances humidity and evaporation.

LITERATURE

On account of the economic importance of grasshoppers a great deal of literature has accumulated since the initial researches in America of Riley, Packard, and Thomas (1877).

Papers that have been most suggestive for the present research are those of Carothers (1923), Hodge (1933), and Criddle (1933a). These investigators studied the feeding and egg laying behavior of a number of acridian species and tested the relations of proper diet to reproduction. As is the case in the investigations here discussed, Carothers and Criddle experimented chiefly with acridians that are not primarily of importance from the economic viewpoint.

⁴The geographical region in question, north central Texas, was in its primitive condition a level to rolling inland prairie. There are no marked variations in altitude. In such an inland region, general climatological conditions are much more uniform than in a mountainous area or even an area with very rough topography.

Recent researches involving problems of physiology, ecology, and control of chiefly economic species have been reported by Parker (1930, 1933), Shotwell (1930, 1935), Langford (1930), List (1934), Faure (1932), Uvarov (1928, 1931), Criddle (1933b), and others. Ecological studies have been made by Vestal (1913), Fox (1914), Morse (1920), and Strohecker (1937).

The extensive literature dealing with taxonomy and distribution of grasshoppers has many references in it to the behavior and feeding habits of grasshoppers. These also at times deal with local and regional distribution, as well as soil relations of individual species. These papers are chiefly the accumulation of field observations and include many of the papers of Hebard, Rehn, Morse, and Blatchley. Many aspects of the problem of *insect feeding* behavior have been investigated by Brues (1920, 1924, 1930, 1936).

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I am greatly indebted to Mary Ellen Douglas for intelligent help with the manuscript, to Dr. Gordon Alexander of the University of Colorado for critically reading the manuscript, and to my wife, Mary N. Isely, for constant volunteer technical assistance in all phases of this research.

EXPERIMENTAL TECHNIQUE

INSECTARY STUDIES

In the experimental studies here undertaken, two major sub-problems were constantly in mind: (1) food preferences and (2) soil choices for oviposition. In controlled experiments attempting to duplicate environmental conditions, it is perfectly obvious that the nearer the experimenter can reproduce the conditions of the natural habitats the more nearly will his results represent conditions as they exist in nature. The cages used in the

⁵ Preliminary Report on Food and Soil Relations of Three Species of Autumn Acridians by Frances Kelly and F. B. Isely. (Abstracts North Texas Biological Society, May 3, 1936).

writer's experiments here reported were designed with this in mind. These tests were conducted in an experimental garden and laboratory at the writer's residence (Figs. 2 and 3).

Cages—Figures 1 and 2 picture the types of cages employed. In large-scale grasshopper experimentation where many specimens are handled, it is necessary to use cages large enough to allow freedom of movement within the cage and small enough to afford opportunity for detailed observations of individual feeding, oviposition, and other behavior activities.

The cage shown in Figure 1 has much to recommend it. The frame and floor of the cage are made of well-seasoned yellow pine. The outside dimensions are 18 x 9 x 15 inches. The ends and back of the cages are covered with a good quality of 16-mesh galvanized screen. The front is

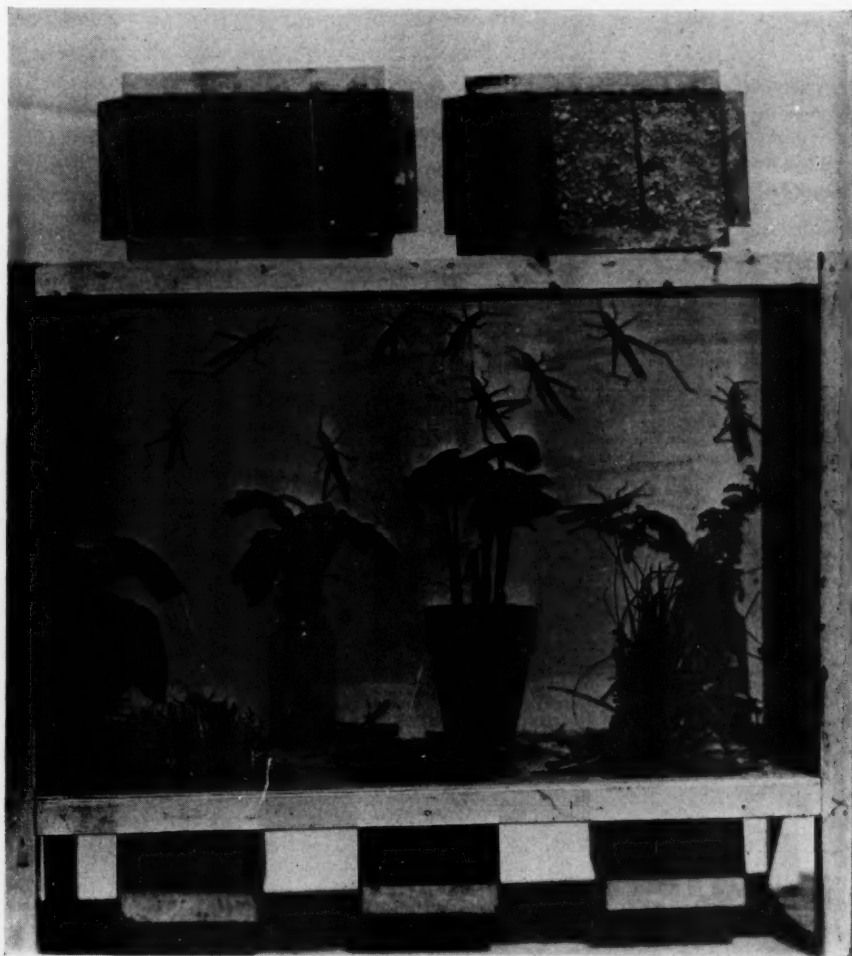


FIG. 1. Regulation cage with sliding glass door. The species shown is *Mermiria maculipennis maculipennis* Bruner. In this arrangement two of the soil pans are holding transplanted vegetation. In the center pan are three different soils as shown in the soil pan on top of the cage, upper right. The different soils were used to test acridian oviposition reactions.

closed with a sliding double strength glass which serves as the door of the cage. The glass front affords excellent opportunity to observe activities. The top and the floor are made of wood, the floor having three openings $5\frac{3}{4} \times 3\frac{1}{4}$ inches into which galvanized pans $5\frac{1}{2} \times 3 \times 3$ inches fit. The pan dimensions do not include the flanges for support. These pans, although used for several purposes, are spoken of in my notes and in this paper as "soil pans." They were found convenient to hold bottles in which cut vegetation was placed in water for food. They also would hold small flower crocks with growing vegetation for food. Sometimes small blocks of soil with grasses or weeds were transplanted into the soil pans. Another important use was the holding of various soils for oviposition choices. In order to supply as wide a range of soils as possible in experiments for soil choices for oviposition, a double division was placed in the soil pan making three compartments for the different soils in a single pan. The compartment arrangement as well as different types of soils are shown in the two pans on top of the cage in Figure 1 and floor plan in Figure 6. This type of cage (Fig. 1) proved very convenient for making food changes. For sanitary reasons in regular routine food preference experiments where large numbers of adult specimens were used, it was found best to transfer specimens from one cage to another every second or third day to permit thorough cleaning of cages. Although we found no difficulty in maintaining seemingly healthful conditions, several species of acridians which we were studying apparently did not thrive in confinement.

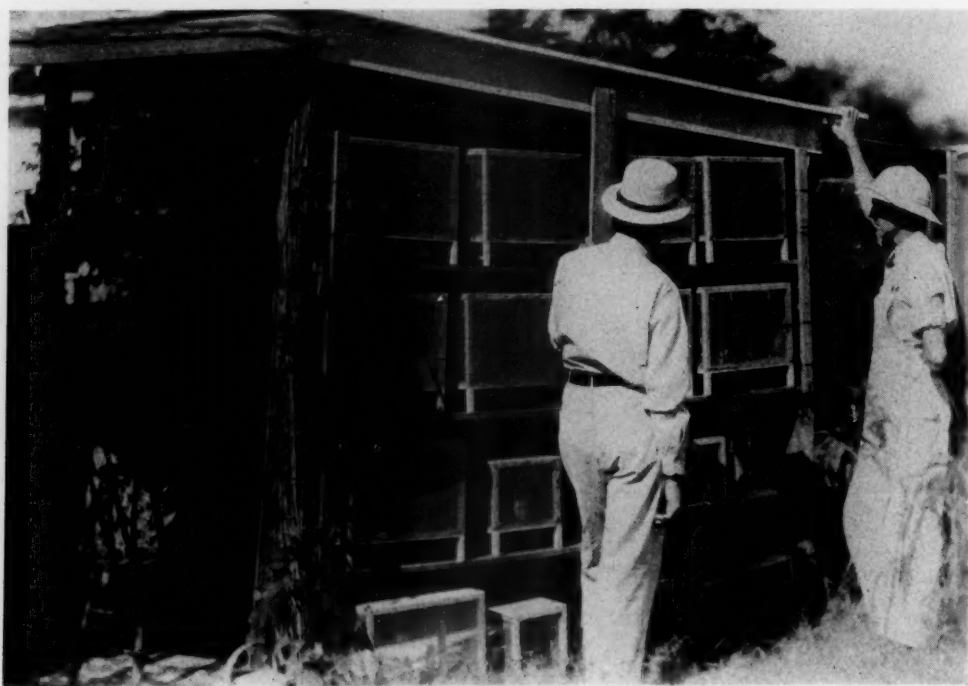


FIG. 2. View of insectary (outdoor laboratory). Larger cages on two upper shelves, smaller cages, lower right.

A similar, smaller cage (Fig. 2, on the bottom shelf) was used for cage studies in the summer of 1935. During 1936-1937 these smaller cages were used when species of which only a few specimens were available for experimentation were handled.

Insectary—Shelter for the cages (Fig. 2) was a necessary feature. While the writer was trying to maintain essentially outdoor conditions, the cover of the shelter supplied needed shade for insects from the intense rays of the mid-day Texas sun and consequent excessive heat during high temperature periods. In the field some grasshoppers (*Cyrtacanthacrinae* and *Acridinae*) climb high into the vegetation on excessively hot July and August days. The *Oedipodinae*, however, are more likely to seek shade nearer the ground.

The insectary shelves afforded space for twenty-four cages. Additional work space was supplied by two tables with shelves underneath, used for cleaning cages and changing specimens.

In addition to the cages, as described above some observations were undertaken in still larger cages. A screened garden enclosure 12 x 30 feet, shown in the forefront of Figure 3, also gave opportunity for studying additional features of acridian behavior.

On account of other duties, the most active period for experimental work was during the months of June, July, and August. However, certain early spring species required study and observation in May, and other late summer species were best checked and observed during September and early

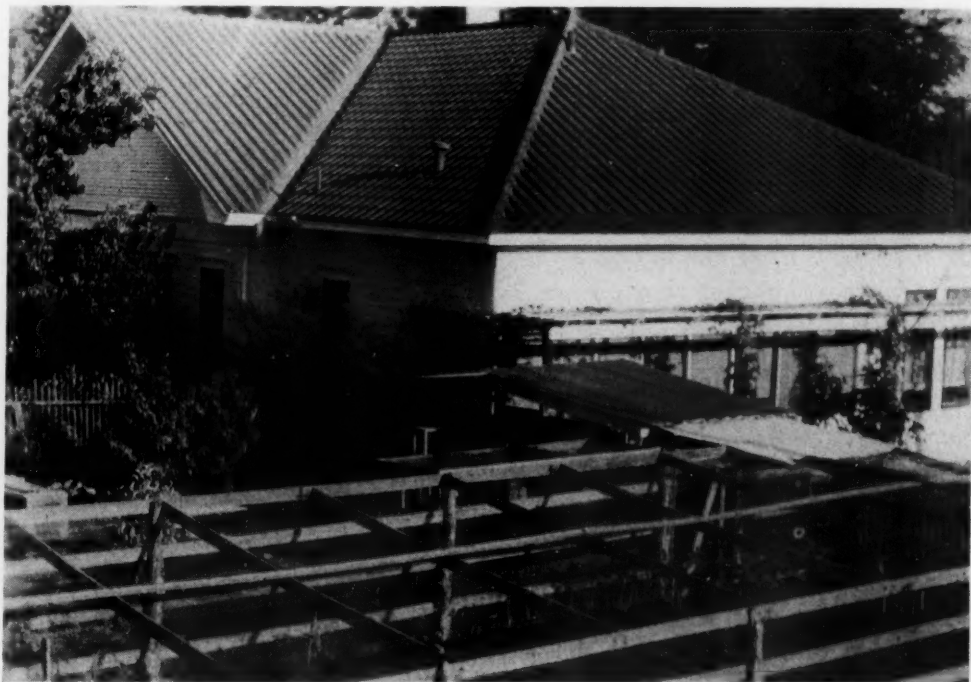


FIG. 3. Garden and Insectary. Screened garden enclosure in the forefront. Other special cages to the left of Insectary.

October. The range of experimentation and observation covered: (1) food choices, (2) feeding behavior, (3) soil choices for oviposition, (4) oviposition behavior, (5) sedentary stridulation,⁶ (6) to a limited extent life history studies, and other behavior activities.

SPECIES OF ACRIDIDAE

In the various experiments undertaken, forty different species of acridians were used.⁷ Adults collected directly from optimum habitats were preferred for behavior experiments although at times experimentation was carried on with late instar juveniles. It is obvious that for the experiments here undertaken, mature specimens fresh from their natural habitats would give the more typical reactions to the tests employed.

HOST-PLANTS

The plant material used involved over 150 different species of the commonest native grasses, forbs,⁸ garden, and crop plants. Many of the plants tested proved to be either unpalatable or unsuited to the dietary needs of the grasshopper species we were studying. In trying to analyze plant and acridian relations on the basis of habitat studies, it seemed obvious that the most important food plants would always be present in the optimum habitats of the various species being studied. However, for several acridian species it proved very difficult to determine a suitable host-plant. Many common acridians were strictly selective in their host-plant preferences. The difficulty of securing host-plants may be illustrated in my experiences with *M. impiger*. In 1936 cage studies *M. impiger* did not thrive. While able to maintain it (keep it alive in fair numbers) for a period of thirty days, the fact that only two packets of eggs were deposited was proof of faulty handling. It should be stated further that one of our difficulties with *M. impiger* was due in part to the fact that its optimum habitats were thirty miles distant from our laboratory. This made it difficult to test a complete series of possible host-plants from the optimum habitat of this species.

As already indicated, the researches of Carothers (1923, p. 8) and Cridle (1933, p. 478) make it evident that for certain acridians only a few plant species, essentially specific, will supply optimum dietary needs for normal growth and reproduction. On the other hand, there are several economic acridian species which are not so restricted. These grasshoppers are apparently adapted to a much wider range of plants (species) as food to meet their dietary requirements for development and reproduction. Hodge (1933, p. 326) shows clearly, however, that even *Melanoplus differentialis* (Thos.) will not develop normally on a restricted diet of oats or lettuce.

⁶ Data concerning sedentary stridulation will be included in a later paper.

⁷ During 1937 in addition to the acridian researches, behavior studies were made of several species of Tettigoniidae.

⁸ The term forb is used to denote native herbs other than grasses (Clements 1929, p. 421). In this paper the terms broad-leaved plants, flowering plants (herbs), and forbs are used as equivalents.

RELATIONS OF ACRIDIDAE TO PLANTS

FOOD HABITS

Our food preference tests show that grasshoppers, like many other groups of insects, fall into three typical classes when experimentally checked for food choices: (1) Many species are oligophagous,⁹ using as food only a limited number of plant species, the plants selected belonging frequently to a single family. (2) A few acridians are essentially monophagous, and their optimum dietary requirements are met by the use of a single plant species for food. (3) Polyphagous species, as would be expected, feed upon both grasses and forbs, and in general select their foods from a wide range of plant species. But even these grasshoppers under normal conditions show food preferences.

FOOD PREFERENCE TESTS

A description of a few typical experiments will make more significant the tabular data which is to follow. Figures 4 and 5 give a photographic record of food selection of characteristic species. The food plants shown on the right were photographed at 10:00 a.m., July 31, 1936. After the picture was

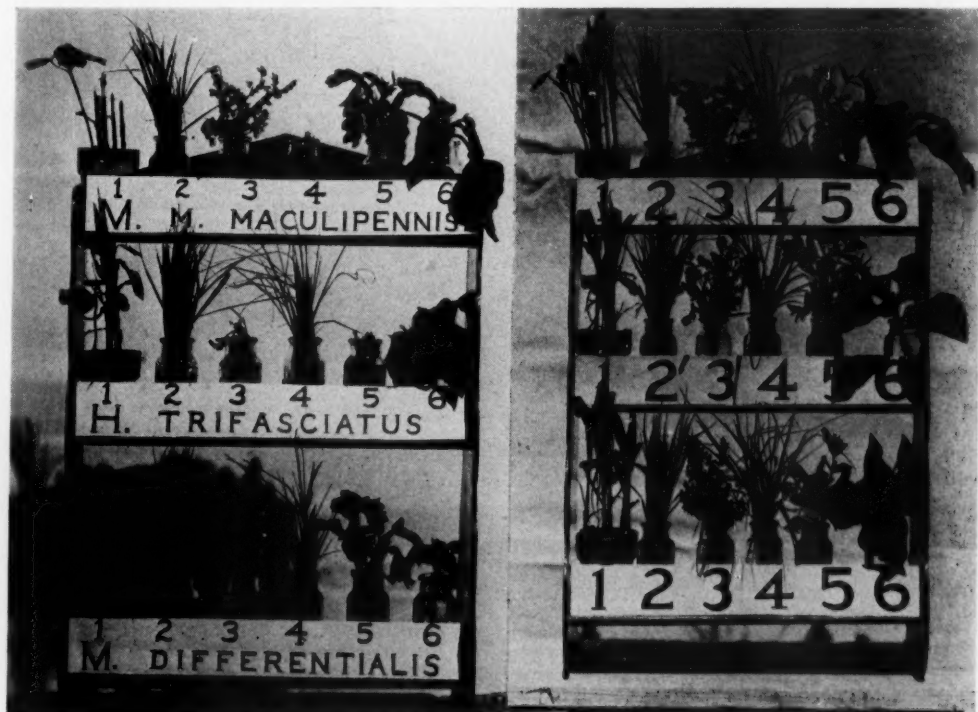


FIG. 4. Photographic record showing food choices of three mid-summer acridians. Identical plant foods were offered to each species as shown on the right. The plants eaten and the results of feeding of each species, 24 hours later, shown on the left.

⁹ "Restricting itself to the members of related plant orders, of a single order, of a single family or even a single genus." (Folsom and Wardle 1934, p. 258).

taken each of the three series of the six different plants was placed in an experimental cage (Fig. 1). Each of these cages contained 25 specimens of one of the three species. The species are named in the left half of Figure 4. The record of the sexes was not definitely checked, but the numbers of males and females were approximately the same. The plants used were as follows: (1) Seedlings grown in a flower pot: cotton (*Gossypium*), corn (*Zea*), and wheat (*Triticum*). The height of the corn seedlings made it necessary to clip the top leaves in order to fit the shelf space used for holding plants to be photographed.

Cut shoots and leaves of the five other food plants were placed in water in bottles when offered as food. These, with the numbers to which they correspond in the figure, are as follows:

- (2) Silver beardgrass—*Andropogon saccharoides* Swartz
- (3) Small leaved spurge—*Euphorbia* sp.
- (4) Bermuda grass—*Cynodon dactylon* (L.) Pers.
- (5) Oval leaved spurge—*Euphorbia nutans* Lag.
- (6) Sunflower—*Helianthus annuus* L.

After twenty-four hours the food plants used in the experiment were again photographed, with the results shown on the left (Fig. 4).

Mermiria maculipennis maculipennis Bruner fed almost exclusively on Bermuda grass, the vegetation in bottle No. 4. Second choices were the wheat seedlings and the leaves of the corn growing in the flower pot (No. 1). There was some feeding on the *Andropogon* (No. 2). The cotton in flower pot No. 1 and the cut shoots of the *Euphorbias* and sunflower in bottles 3, 5, and 6 were untouched.

Hadrotettix trifasciatus (Say) fed especially on the two species of *Euphorbia* (Nos. 3 and 5). The figure shows that the vegetation in these plants was eaten to the rim of the bottles. Other vegetation was untouched. These two spurges are not usually found in the optimum habitats of *H. trifasciatus*. This feeding behavior represents a good case of adaptation to new food plants under cage environments.

The first choice of *Melanoplus differentialis* (Thos.) centered around the cultivated crop plants growing in the flower pot (No. 1). There was considerable feeding on the sunflower (No. 6) and on *Euphorbia* (No. 3). There was a little feeding on *Andropogon* (No. 2). Bermuda grass (No. 4) and *E. nutans* (No. 5) were untouched.

The set-up for the experiments, for which Figure 5 is a photographic record, represents the feeding activities of four species that reach their adult peak in north central Texas in August.

In these experiments an identical set-up of plant foods was arranged and photographed as shown in bottles in Figure 5, upper left Nos. 1-6. Unfortunately Nos. 3 and 5 in the upper left were reversed in the arrangement shown in the upper right. The upper right photograph merely shows the

way in which the plants were placed in the soil pans. The significant numbers to be studied for comparison are the ones shown in the upper left series. The plants used were as follows:

- (1) Broomweed—*Amphiachyris dracunculoides* (DC.) Nutt.
- (2) Johnson grass—*Sorghum halepense* (L.) Pers.
- (3) Common ragweed—*Ambrosia psilostachya* DC.
- (4) Silver beardgrass—*Andropogon saccharoides* Swartz.
- (5) Giant ragweed—*Ambrosia aptera* DC.
- (6) Bermuda grass—*Cynodon dactylon* (L.) Pers.

The photographed series (Fig. 5) was set up September 29, 1936. Similar set-ups of food plants as nearly identical as possible were placed with each of the four acridian species in four separate standard cages. The numbers of specimens used were as follows:

Syrbula admirabilis Uhler—12

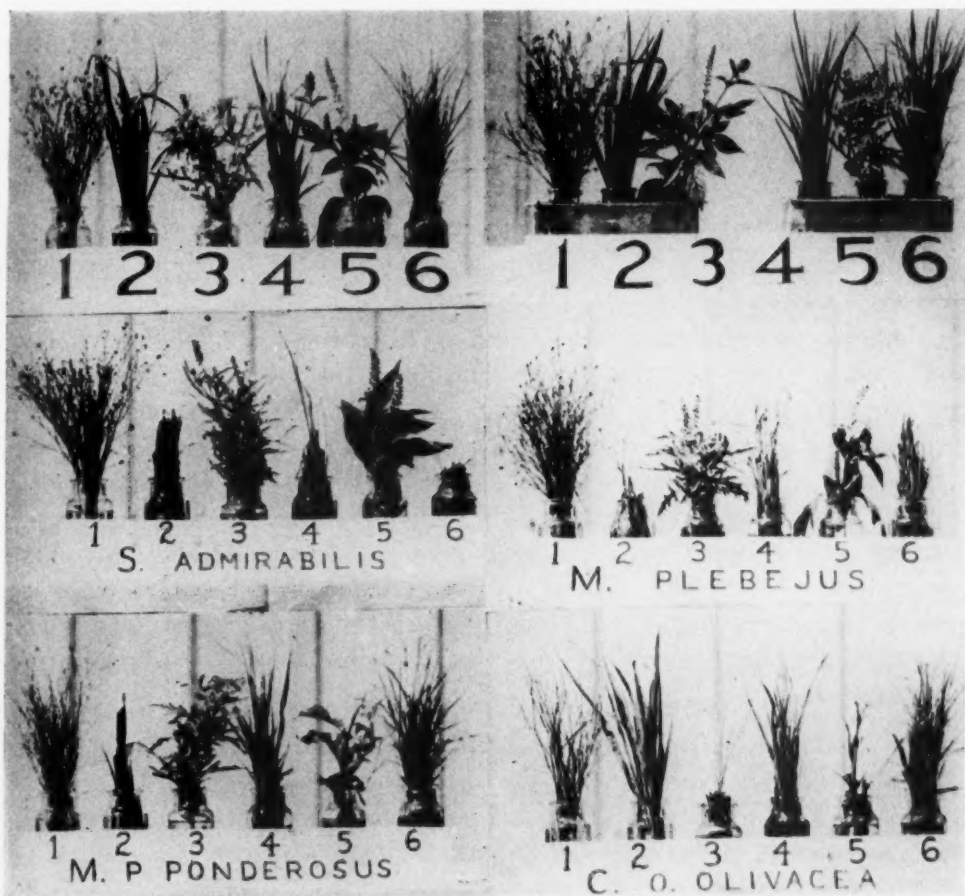


FIG. 5. Photographic record showing the feeding activities of four species of grasshoppers which reach their adult peak in north central Texas in August. Typical plant arrangement upper left. Food bottles in soil pans, upper right. The plants eaten and those not eaten are shown below and arranged in same order as 1-6 upper left.

Melanoplus plebejus (Stål)—14

Melanoplus ponderosus ponderosus Sc.—11

Campylacantha olivacea olivacea Sc.—14

Most of these specimens were females. Soon after this series of experiments was arranged (September 29) the weather became unfavorable, turning cold and rainy. For the first three days the grasshoppers were more or less dormant, but with sunshine and warm weather on the fourth day (October 2) feeding activities were renewed. The food preference results (Fig. 5) were photographed at noon, October 3. The appearance of the control set-up of plants and the plants not eaten in the cages shows that the vegetation kept fresh and in good condition during the period of experimentation (September 29-October 3).

The first choice of *Syrbula admirabilis* Uhler was Bermuda grass (No. 6). After the Bermuda grass was eaten *S. admirabilis* fed on Andropogon (No. 4) and Johnson grass (No. 2). This species did not touch the forbs.

Melanoplus plebejus (Stål) showed a definite preference for Johnson grass (No. 2). Second choices were Andropogon (No. 4) and Bermuda grass (No. 6). All of its food plants were grasses.

Melanoplus ponderosus ponderosus Sc.—This species is a flower and fruit feeder. Flowers and fruit were stripped from broomweed (No. 1) and giant ragweed (No. 5). However, this species did not touch the common ragweed (No. 3). It fed to an extent on the foliage of the plants of Johnson grass (No. 2) and giant ragweed (No. 5).

Campylacantha olivacea olivacea Sc.—This species also feeds on flowers and fruit. It stripped the flowers and fruit from broomweed (No. 1), common ragweed (No. 3), and giant ragweed (No. 5). First choice foliage for *C. o. olivacea* was *Ambrosia psilostachya* DC. This common ragweed was usually untouched in the other acridian cages in our continuous series of food preference experiments. This widely distributed plant, however, is a coarse, sturdy weed which is used quite extensively by several acridian species for roosting and shelter. Even in the cage occupied by *Syrbula admirabilis* Uhler (Fig. 5), although the grasses were used as food, roosting, when the grasshoppers were inactive, was done on the cut shoots of the two ragweeds.

DETAILED EXPERIMENTAL STUDY OF ACRIDIAN HOST-PLANT PREFERENCES

ORGANIZATION OF DATA

The foregoing account (Food Preference Tests) and the photographic records should serve to make clear the data pertaining to food choices given in Tables 1-3. The abbreviations used in the tables are explained in connection with a complete listing of Acrididae and host-plant species.

All plants specifically listed in the tables were found to be acceptable food for one or more species of grasshoppers. Host-plants listed for Table 1 are not repeated in the additional host-plant species listed for later tables. Terms and keys used in Tables 1-3 are fully explained in a general account preceding Table 1. The key meanings are briefly repeated in connection with each table.

FORM OF PLANT FOOD

As a rule the food was supplied in the form of cut shoots of grasses and forbs. The cut shoots were immediately placed in bottles of water after being cut. Sometimes the food was changed during the day, but usually only once daily.

Crop Plants. On account of possible economic importance, crop plants, especially wheat, corn, and cotton were always checked as to their acceptability as food. Crop plants as food were offered in two forms: (1) as cut shoots and, more frequently, (2) as seedlings in small flower pots. Since the reactions of the acridians were essentially similar, these differences in the crop-plant food materials are not taken into account in the tables. In the discussion of individual species, differences in reaction may be noted. The determined host-plants of experimental species were offered, as nearly as possible, as food to other acridians being checked at the same time for food choices. Since the chief experimental work was in progress for six months of the year, many native weeds and grasses were not in season at the time a specific acridian species was being studied. As a result, host-plants of one species were not always available to be offered to other species being tested.

TERMS USED IN TABLES 1-3

HP—Host-Plant. This designation is used for plants which were *repeatedly selected as food* by an acridian being tested. It also means that the plant species is *available in the optimum habitats* of this acridian as determined by field studies.

PH—Primary Host. Cage and field studies in several instances pointed to specific plant species as essential to maintenance of certain acridian species. These plants are designated as primary hosts.

1—First Choice. This designation means that the food plant was eaten in preference to all others by the acridian species being tested. It may include host-plants, but usually host-plants are designated by HP. Primary host-plants naturally would be first choice. If they were found to be primary host-plants, they are designated by PH in the tables.

1-2, 1-3. These designations indicate that the plant species was eaten freely. The order of preference may have been variable in our long series of tests. Several species were under observation in cages for over two months in one season. Others were rechecked for food preferences three different years. The 1-2, 1-3 designations are especially used for crop-plant preferences.

2—Second Choice. If food plant No. 1 was available in a cage, a plant freely eaten after the supply of No. 1 was exhausted is designated as choice No. 2. For some of our tests No. 2 is apparently one of the host-plants of the species being tested.

3—Third Choice. Third choice plants are probably not especially desirable for the species in question. Third choice means that these plants were eaten when other more desirable food was no longer available.

St—Starved with this plant available. These data were secured from starvation experiments, Tables 4-6.

N—Nibbled. The term nibbled is reserved for plants that were eaten very sparingly or barely nibbled.

R—Refused. The term refused is used for plants that were not eaten. In our tests certain acridian species absolutely refused many different plant species offered as food.

Fl—Flowers. Flowers, especially ray and disk flowers of Compositae, were eagerly eaten by several grasshopper species.

Fr—Fruit. A few species fed on immature fruit, usually along with foliage.

Others Refused. Since lack of space prevents the listing of all of the plant species tested, the designation "Others Refused" affords opportunity to show in the tables the total number of plant species offered as food. With the exception of crop plants, as a rule only plants from optimum habitats of an acridian species were offered. However, plants acceptable to other acridian species, and available, were usually tested.

Others Eaten. These are also plants that are not listed in the tables and figure only in the totals of plants species offered. Here are included garden plants, grasses, and weeds easily available.

Number of Days Studied. The total days an individual species was under observation in cage tests is given.

Since there is an evident parallel between feeding behavior and sub-family grouping, advantage has been taken of this correlation in arranging the food preference data which follow under the three different acridian sub-families concerned.

ACRIDINAE

HOST-PLANTS OF ACRIDINAE

The probable host-plants were selected by making field lists¹⁰ of available plants in optimum habitats of the grasshoppers being experimentally checked for food choices. Many plants were offered as food which were universally refused in routine tests. Time was not available to resort to starvation tests with many of these plants which were rejected. Only the totals of the plant species which proved wholly unpalatable are given in connection with the tables.

¹⁰ Identifications of host-plant species were checked by comparison with herbarium specimens identified by plant taxonomists.

In the tables the plant species are usually listed by their generic names. However, crop plants and certain well known grasses and weeds are listed by common name (Bermuda grass, Johnson grass, broomweed, sunflower, etc.).

MONOCOTYLEDONS— <i>Species</i>	<i>Common Name</i>
<i>Andropogon furcatus</i> Muhl.....	Bluejoint Turkeyfoot
<i>Andropogon saccharoides</i> Swartz.....	Silver Beardgrass
<i>Cynodon dactylon</i> (L.) Pers.....	Bermuda Grass
<i>Stipa leucotricha</i> Trin. and Rupr.....	Texas Needlegrass
<i>Sorghum halepense</i> (L.) Pers.....	Johnson Grass
<i>Sporobolus heterolepis</i> A. Gray.....	Prairie Dropseed

CROP PLANTS

<i>Triticum</i> sp.....	Wheat
<i>Saccharum officinarum</i> L.....	Sugarcane
<i>Zea mays</i> L.....	Maize, Indian corn

DICOTYLEDONS

<i>Evax multicaulis</i> DC.....	Indian Tobacco
<i>Amphiachyris dracunculoides</i> (DC.) Nutt.....	Broomweed
<i>Helianthus annuus</i> L.....	Sunflower
<i>Plantago</i> sp.....	Plantain

CROP PLANTS

<i>Gossypium hirsutum</i> L.....	Cotton
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The plants listed above were found to be acceptable food for at least one of the ten different acridian species listed below.

In the series of experiments with these Acridinae eight additional monocotyledons and fourteen additional dicotyledons were repeatedly offered as food to several species of the Acridinae and were refused.

SLANT-FACED GRASSHOPPERS—ACRIDINAE

<i>Species</i>	<i>Abbreviations in Table</i>
1. <i>Mermiria maculipennis maculipennis</i> Bruner.....	M. mac.
2. <i>Mesochloa abortiva</i> Bruner.....	
3. <i>Acrolophitus variegatus</i> (Thos.).....	A. var.
4. <i>Syrbula admirabilis</i> Uhler.....	S. ad.
5. <i>Amphitornus coloradus</i> (Thos.).....	
6. <i>Orphulella speciosa</i> (Sc.).....	
7. <i>Geneotettix deorum</i> (Sc.).....	G. deo.
8. <i>Boopedon nubilum</i> (Sc.).....	B. nub.
9. <i>Boopedon maculatum</i> Caudell.....	B. mac.
10. <i>Boopedon auriventris</i> McNeill.....	B. aur.

The feeding reactions of the seven of these species of the Acridinae indicated by abbreviations are tabulated in Table 1. Further discussion of feeding behavior follows the table.

TABLE 1. FOOD PREFERENCES OF ACRIDINAE

HP—Host-Plant.
PH—Primary Host.
1—First Choice.
1-2,1-3—Eaten in absence of 1
or HP.

2—Second Choice.
St—Starved.
N—Nibbled.
R—Refused.
--—Not tested.

Acridinae Tested	M. mac.	A. var.	S. ad.	G. dec.	B. nub.	B. mac.	B. aur.
Number of days studied . . .	64	62	47	46	19	25	4
PLANTS TESTED							
<i>A. furcatus</i>	2	R	2	--	N	1-3	HP
<i>A. saccharoides</i>	2	R	2	N	R	1-3	PH
Bermuda grass	1	R	1	1	HP	HP	?
<i>Stipa</i>	1-3	R	2	--	N	1-3	--
Johnson grass	1-2	N	1-3	1-3	N,R	1-2	N
<i>S. heterolepis</i>	HP	--	2	2	--	--	--
Crop Plants							
Wheat	1-2	St	1-2	1-2	R	1-2	--
Cane	1-3	St	1-3	1-3	--	--	--
Corn	1-3	R	1-3	1-3	--	--	--
Forbs							
<i>Evax multicaulis</i>	R	PH	--	--	--	--	--
Broomweed	St	--	St	R	R	R	--
Sunflower	St	R	St	R	R	R	R
<i>Plantago</i>	--	2	--	--	--	--	--
Crop Plants							
Cotton	R	R	R	R	R	R	--
Total Eaten	8	4	8	5	1	6	3
Total Refused, Nibbled, Starved	4	8	3	4	8	3	2
Others Refused (Not in table)	26	11	15	5	2	6	4
Others Eaten (Not in table)	6	2	2	0	2	4	1
Grand Total	44	25	28	14	13	19	10

FEEDING BEHAVIOR OF THE ACRIDINAE

The ten species of the sub-family Acridinae studied in food tests show a 90% preference for grasses as host-plants. Bermuda grass easily ranks as the first choice. The preference for Bermuda grass¹¹ on the part of our Acridinae was acquired. It is obvious, as already suggested, that vegetation *absent in typical virgin, optimum habitats* of a species can not, as a matter of course, belong to the original basic food requirements of the species.

Some of the facts of our feeding behavior studies are represented in a brief review of the feeding activities of *Mermiria maculipennis maculipennis* Bruner. This characteristic blackland prairie species was under constant

¹¹ Miss Agnes Chase, Senior Agrostologist, Bureau of Plant Industry, writes under date of July 30, 1937: "Bermuda grass, *Cynodon dactylon* (L.) Pers., must have been introduced with the first Spanish explorers." "The first record I find of *Cynodon* in America is in Pursh's *Flora Americae Septentrionalis*, 1814. He says, 'on roadsides and in cultivated ground frequent.'"

observation in cages from the time it reached maturity, June 24, to August 4, 1936. Preliminary studies of this species had already been made in 1935, and a brief recheck was made in 1937. *M. m. maculipennis* was given a thorough testing in our experiments for both food preferences and soil choices in oviposition. During the 1936 studies about thirty individuals were constantly maintained in a single cage (Fig. 1). In their optimum habitats the Andropogons (*A. furcatus* and *A. saccharoides*) afford shelter and roosting surfaces for these agile, elongated, slant-faced grasshoppers. The Andropogons undoubtedly are the important field index plants of *M. m. maculipennis*. While they are acceptable as food they are not the primary host-plants if the results of cage studies are taken as evidence.

In cages *Mermiria m. maculipennis* definitely chose Bermuda grass and Sporobolus for food in preference to either of the species of Andropogon. In some tests it appeared that young leaves of Johnson grass were more largely eaten than the Andropogons.

On July 22, and again on July 24 and 29, 1937 I made a thorough examination of a recently discovered habitat, a long, narrow strip of railroad right-of-way¹² blackland prairie land. For a distance of about five yards on either side of the railroad tracks the made-soil was covered with a heavy stand of Johnson grass with a few intermixed weeds. This inner strip on either side of the railroad track is the ground that is continually disturbed in upkeep-operations of the railroad section hands, such as cutting of weeds and grading. Outside of this inner belt was a strip five to eight yards in width of undisturbed prairie land.¹³ The vegetation of this outer belt was predominantly native grasses mixed with weeds. *Mermiria maculipennis maculipennis* Bruner was fairly abundant in this outer belt. The inner belt of Johnson grass was inhabited by larger numbers of *Melanoplus differentialis* (Thos.). Infrequent representatives of several other acridians were noted. The differences in distribution were clean-cut. The *M. m. maculipennis* were feeding by preference on native grasses (Sporobolus, Andropogon, grama). The *M. differentialis* were using as food some Johnson grass but especially the mixed weeds of this inner belt. These field observations are given with some detail to emphasize the fact that cage results¹⁴ need to be counter-checked with field observations.

An exceptional species among our Acridinae from the viewpoint of food preferences was *Acrolophitus variegatus* (Thos.). In Manitoba, Canada, Criddle (1933, p. 481) reports *A. hirtipes* (Say) feeding by preference on the Boraginaceae. During 1935 it was difficult to maintain *A. variegatus*

¹² A railroad right-of-way field station has in itself many artificial restrictions when viewed as a natural environment.

¹³ The once virgin blackland prairie of north central Texas is now nearly wholly given over to agriculture.

¹⁴ In special cages (40 x 20 x 30 inches high) and in larger soil pans blocks of soil of Andropogon and Sporobolus were transplanted in one end and Johnson and sunflower blocks in the other end. Forty specimens of each species were placed in this cage. Over 80 per cent of the *Mermiria maculipennis maculipennis* Bruner selected the Andropogon end of the cage while the *Melanoplus differentialis* (Thos.) showed an even stronger preference for the Johnson grass end. The test suggested the advantage of larger cages for behavior studies.

successfully in cages on a diet of various grasses and forbs. May 16, 1936 on a field study trip I observed a small colony of fifth instar juveniles associated with *Evax multicaulis* DC. Cage tests and repeated field observations proved this plant to be the primary host-plant of *A. variegatus*. Plantain (*Plantago*) is a second choice food plant for this species.

An excerpt from my field and laboratory notes will further suggest the need of correlation between field and laboratory studies. Field Station, Lancaster, Dallas County, Texas, May 16, 1936: "After a thorough examination of the flora of what appears to be an optimum habitat of *A. variegatus* it appears that Indian tobacco (*Evax multicaulis* DC.) should be given tests as a likely food for this species. The juvenile and the adult color pattern of this acridian with its pale green ground-color, mottled with white and the white woolly stems and the broad leaves of *Evax* suggest a background which fits very well into the general picture of protective coloration."

Laboratory notes, May 20, 1936: "After four days testing with fifteen specimens freshly brought in from the field, it is clear that *A. variegatus* feeds by choice and perhaps almost exclusively in its juvenile stages on *Evax*. All of its feeding for a period of four days has been exclusively on *Evax*, and as nearly as can be determined not a nibble has been taken off of the various grasses and other forbs in the food bottles in the cage."

Syrbula admirabilis Uhler—This is one of the most generally distributed late summer and fall grasshoppers in our area. The results of experimental studies suggest that it is a general grass feeder. Bermuda grass is ranked as the first choice and *S. admirabilis* is often found associated with Bermuda grass in nature. It is also frequently associated with *Andropogon* and *Sporobolus*.

Geneotettix deorum (Sc.) is one of the most widely distributed summer and early fall acridians. However, in north central Texas it seldom becomes abundant in any single locality. Bermuda grass was ranked as first choice in cage tests but all of the field data suggest that *G. deorum* has a wider choice of grasses than our experimental data would indicate.

Little can be added to the facts in the table concerning the *Boopedona*. These three species were not as extensively studied as some of the others. *Boopedon auriventris* McNeill is of interest in that it was one of two grass feeding species which in cage tests did not select Bermuda grass as its first choice.

In addition to the seven species listed in the table, food choice studies were undertaken with *Mesochloa abortiva* Bruner, *Amphitornus coloradus* (Thos.), and *Orphulella speciosa* (Sc.). As the series of checked experiments was not as extensive as for the other seven Acridinae, details are not given in the tables. These relatively small Acridinae belong definitely to the grass feeders with Bermuda grass ranking as first choice. In the case of *O. speciosa* Bermuda grass appears to be the present host species in north central Texas.

OEDIPODINAE AND BATRACHOTETRIGINAE

ADDITIONAL HOST-PLANTS OF THE OEDIPODINAE

MONOCOTYLEDONS— <i>Species</i>	<i>Common Name</i>
<i>Aristida purpurea</i> Nutt.....	Purple Three-Awn
<i>Bromus catharticus</i> Vahl.....	Rescue Grass
<i>Cenchrus</i> sp.	Sandbur

DICOTYLEDONS

<i>Gaillardia pulchella</i> Foug.....	Indian Daisy
<i>Salvia farinacea</i> Benth.....	Blue Salvia
<i>Monarda clinopolioides</i> A. Gray.....	Horse Mint
<i>Asclepiodora decumbens</i> (Nutt.) A. Gray.....	Milkweed
<i>Euphorbia</i> sp.	Small leaved spurge
<i>Euphorbia nutans</i> Lag.....	Oval leaved spurge
<i>Jatropha stimulosa</i> Michx.....	Bull nettle
<i>Houstonia angustifolia</i> Michx.....	Houstonia
<i>Hymenopappus corymbosus</i> T. & G.....	Hymenopappus
<i>Ambrosia psilostachya</i> DC.....	Common ragweed
<i>Ambrosia aptera</i> DC.....	Giant ragweed

For other plant species listed in Table 2 see plants previously listed for Table 1.

BAND-WINGED GRASSHOPPERS—OEDIPODINAE

<i>Species</i>	<i>Abbreviations in Table</i>
1. <i>Arphia simplex</i> Sc.....	A. sim.
2. <i>Chortophaga viridifasciata</i> (DeGeer).....	
3. <i>Encoptolophus subgracilis</i> Caudell.....	
4. <i>Encoptolophus sordidus costalis</i> (Sc.).....	
5. <i>Hippiscus rugosus</i> (Sc.).....	
6. <i>Pardalophora saussurei</i> (Sc.).....	P. sauss.
7. <i>Xanthippus corallipes pantherinus</i> (Sc.).....	X. c. p.
8. <i>Spharagemon collare cristatum</i> (Sc.).....	S. cris.
9. <i>Trachyrhachis kiowa fuscifrons</i> (Stål).....	
10. <i>Trimerotropis citrina</i> Sc.....	
11. <i>Trimerotropis pistrinaria</i> Sauss.....	T. pist.
12. <i>Hadrotettix trifasciatus</i> (Say).....	H. tri.

LUBBER GRASSHOPPER—BATRACHOTETRIGINAE

1. *Brachystola magna* (Girard)

The food preferences of six of the above Oedipodinae are shown in Table 2. The other species are included in the discussion that follows Table 2.

FEEDING BEHAVIOR OF THE OEDIPODINAE AND BATRACHOTETRIGINAE

The Oedipodinae listed in Table 2 were given a rather thorough checking as to their food preferences. Three species are primarily grass feeders: *Arphia simplex* Sc., *Pardalophora saussurei* (Sc.), and *Xanthippus corallipes pantherinus* (Sc.). Two others, *Trimerotropis pistrinaria* Sauss. and

TABLE 2. FOOD PREFERENCES OF OEDIPODINAE

HP—Host-Plant.
PH—Primary Host.
1—First Choice.
1-2,1-3—Eaten in absence of 1
or HP.

2—Second Choice.
3—Third Choice.
St—Starved.
N—Nibbled.
R—Refused.
--—Not tested.

Oedipodinae Tested	A. sim.	P. sauss.	X. c. p.	S. cris.	T. pist.	H. tri.
Number Days Studied.....	62	104	98	30	92	83
PLANTS TESTED						
Grasses						
<i>A. furcatus</i>	N	1-3	N	2	R	R
<i>A. saccharoides</i>	1-2	1-3	HP	2	St	R
<i>Aristida purpurea</i>	1-2	1-3	HP	N	N	N
<i>Bromus catharticus</i>	1-2	1-3	1-3	--	--	--
Bermuda grass.....	1	1	1	1	3	3
<i>Stipa</i>	HP	1-3	1-3	1-2	--	R
Johnson grass.....	1-2	1	1-3	1	3	3
Sandbur.....	--	1	--	1-3	--	--
Crop Plants						
Wheat.....	1	1-2	1-3	1-3	2	3
Corn.....	1-2	1-3	N	N	R	N
Forbs						
Sunflower.....	N	N	N	N	St	N
Broomweed.....	R	R	N	--	St	St
<i>Gaillardia</i>	R	R	R	--	2	N
<i>Monarda</i>	R	R	R	R	--	R
<i>A. decumbens</i>	R	--	R	--	R	HP
Bull nettle.....	--	N	--	1-2	--	--
<i>Houstonia</i>	R	--	--	--	HP	HP
<i>Hymenopappus</i>	R	--	--	--	PH	R
Common Ragweed.....	St	--	R	--	St	St
Giant Ragweed.....	St	R	R	R	N	St
Crop Plants						
Cotton.....	R	N	N	1-3	N	N
Total Eaten.....	8	10	7	9	5	3
Total Nibbled, Refused, Starved.....	11	7	10	5	10	13
Others Refused (Not in table).....	21	16	8	8	8	34
Others Eaten (Not in table).....	9	9	11	7	7	11
Grand Total.....	39	42	36	29	40	51

Hadrotettix trifasciatus (Say) definitely select the foliage of certain dicotyledons as food. *Spharagemon collare cristatum* (Sc.), to the extent of our tests, should be classed as a mixed feeder, that is, selecting both grasses and forbs.

Stipa leucotricha Trin. and Rupr. is clearly the major host-plant in optimum habitats of *A. simplex*. *A. simplex* in north central Texas hatches with the fall rains usually in September and early October. It passes the period from October to March as a first instar juvenile. Shelter undoubted-

ly plays a very important role in affording favorable environmental conditions for this species. *A. simplex* is a strong direct flier and in its adult stage is rather widely distributed. The juveniles, however, are found in large numbers only in open woods and timber margins.

Xanthippus corallipes pantherinus (Sc.) passes its first instar stages, September to April, in exposed situations. Thin soil (Houston stony clay shallow phase), hill tops and eroded (subsoil) slopes are the selected sites for egg laying. The juveniles through the various instars apparently remain near the hatching sites. As adults, however, *X. c. pantherinus* seeks the taller vegetation. This species is noteworthy as a strong, direct flying species.

The feeding behavior of *Pardalophora saussurei* (Sc.) paralleled very closely that of *X. c. pantherinus*. However, the optimum habitats of these two species are very different. In the second section of this paper the reasons for differing habitats of *X. c. pantherinus* and *P. saussurei* will be discussed.

Continued and persistent studies were carried on with *Trimerotropis pistrinaria* Sauss. and *Hadrotettix trifasciatus* (Say). *T. pistrinaria* is limited in its field distribution to eroded subsoils. It is able to exist apparently on a very sparse diet. As shown in the table, *Hymenopappus* served as a host-plant of this species. This plant is abundant in the optimum habitats of *T. pistrinaria*. *Houstonia* was the No. 2 choice from among a large group of plants offered to *T. pistrinaria*. Field behavior of *T. pistrinaria* is of interest. It belongs to that group of acridians that circle back in their flight thus showing a definite site-selection. The "circle back" type of flight behavior is characteristic of those acridians that stick rather closely to their specific soil backgrounds as adults. In contrast with these we have such species as *A. simplex*, *X. c. pantherinus* among the Oedipodinae, and *Mermiria maculipennis maculipennis* Bruner among the Acridinae, which usually fly straight away when flushed. The latter species are more likely to become widely scattered as adults.

Hadrotettix trifasciatus (Say) is somewhat similar in its choice of habitat to *Trimerotropis pistrinaria* Sauss., but ranges more widely. Our field studies pointed out *Asclepiodora decumbens* (Nutt.) A. Gray and *Houstonia angustifolia* Michx. likely food selections. Later cage studies proved that these plants were eagerly fed upon by *H. trifasciatus*. In spite of long and persistent experimentation, there still remains a great deal to be done in determining the host-plants of this species.

Six other Oedipodinae were checked for food preferences. Cage tests were carried on with these species for only brief periods, but the records show that all six species are essentially grass feeders. Further study will doubtless bring out significant variations. *Encoptolophus subgracilis* Caudell is of special interest because it is the only grasshopper in our area that confines its activities to cultivated fields. In our cages it fed on the grasses growing as weeds in field margins and to a limited extent on the leaves of

cotton. However, the damage it does to the cotton is negligible. *Trimerotropis citrina* Sc. also is a mixed feeder. Bermuda grass, Parthenium, giant ragweed, and broomweed were found to be acceptable food plants for *T. citrina*.

In our cages *Encoptolophus sordidus costalis* (Sc.), *Chortophaga viridifasciata* (DeGeer), *Hippiscus rugosus* (Sc.), and *Trachyrhachis kioewa fuscifrons* (Stål) fed chiefly on grasses.

Brachystola magna (Girard) is one of the economic species of certain areas of Texas. In the field it is very definitely associated with coarse weeds and in the cages fed by preference on cotton, sunflower and giant ragweed.

CYRTACANTHACRINAE

ADDITIONAL HOST-PLANTS OF CYRTACANTHACRINAE

DICOTYLEDONS—Species	Common Name
<i>Centaurea americana</i> Nutt.	Star Thistle
<i>Thelesperma trifidum</i> (Poir.) Britton	
<i>Engelmannia pinnatifida</i> T. & G.	
<i>Baccharis texana</i> (T. & G.) Gray	Dactylotum weed
<i>Aster exilis</i>	Aster
<i>Grindelia</i>	Gumweed
<i>Parthenium hysterophorus</i> L.	Parthenium

For other plants listed in Table 3 see lists of plants given in connection with Tables 1 and 2.

SPINE-BREADED GRASSHOPPER—CYRTACANTHACRINAE

Species	Abbreviations in Table
1. <i>Hypochlora alba</i> (Dodge)	
2. <i>Paraideмона punctata</i> (Stål)	P. punc.
3. <i>Campylacantha olivacea olivacea</i> Sc.	C. o. o.
4. <i>Hesperotettix viridis viridis</i> (Thos.)	H. v. v.
5. <i>Hesperotettix speciosus</i> (Sc.)	H. spec.
6. <i>Melanoplus scudderi latus</i> Morse	
7. <i>Melanoplus texanus</i> (Sc.)	M. tex.
8. <i>Melanoplus plebejus</i> (Stål)	M. pleb.
9. <i>Melanoplus discolor</i> (Sc.)	
10. <i>Melanoplus flabellatus</i> (Sc.)	M. flab.
11. <i>Melanoplus differentialis</i> (Thos.)	M. dif.
12. <i>Melanoplus ponderosus ponderosus</i> (Sc.)	M. pon.
13. <i>Melanoplus confusus</i> (Sc.)	M. con.
14. <i>Melanoplus mexicanus mexicanus</i> (Sauss.)	
15. <i>Melanoplus keeleri keeleri</i> (Thos.)	
16. <i>Melanoplus impiger</i> (Sc.)	M. imp.
17. <i>Dactylotum pictum</i> (Thos.)	D. pic.

FEEDING BEHAVIOR OF THE CYRTACANTHACRINAE

Many of the Cyrtacanthacrinae tested in our cages proved to be almost entirely selective feeders. Of the twelve species shown in Table 3 all but

TABLE 3. FOOD PREFERENCES OF CYRTACANTHACRINAE

HP — Host-Plant.
 PH — Primary Host.
 1 — First Choice.
 1-2, 1-3 — Eaten in absence of 1 or HP.

2 — Second Choice.
 3 — Third Choice.
 St — Starved.
 N — Nibbled.
 R — Refused.

Fl — Flowers.
 Fr — Fruit.
 -- — Not tested.

Cyrtacanthacrinae Tested	P. punc.	C. o. o.	H. v. v.	H. spec.	M. tex.	M. pleb.	M. flab.	M. dif.	M. pon.	M. con.	M. imp.	D. pic.
Number Days Studied.	48	46	67	66	56	29	46	55	49	42	52	51
PLANTS TESTED												
Grasses												
<i>A. saccharoides</i>	St	St	St	St	St	2	R	N	R	St	R	R
Bermuda grass.	St	N	St	St	St	1-3	2	3	3	St	R	R
<i>Stipa</i>	R, N	--	--	--	R	--	N	N	--	St	R	R
Johnson grass.	R, N	R	R	R	3	1	3	HP	2	3	N	N
Crop Plants												
Wheat.	N	--	R	R	3	--	2	1-3	--	1-3	1-3	3
Corn.	1-3	--	R	R	3	2	3	1-3	2	N	1-3	3
Forbs												
Broomweed.	3	Fl	HP	--	3	Fl	N	1-3	Fl	--	N	3
<i>Centaurea</i>	R	--	--	R	3	--	Fl	1-3	--	N	1-3	--
<i>Gaillardia</i>	HP	--	N	N	HP	3	N	1-3	N	Fl, N	Fr 3	--
<i>Thelesperma</i>	HP	--	--	--	2	R	--	--	R	Fr	R	--
<i>Engelmannia</i>	2	--	--	--	3	--	HP	R	--	--	--	--
<i>Baccharis</i>	N	R	R	--	N	R	--	N	R	--	--	PH
<i>Aster</i>	--	R	1-3	1-3	--	3	3	1-3	3	--	3	HP
<i>Grindella</i>	R	R	HP	N	R	R	N	1-3	R	--	R	R
<i>Parthenium</i>	--	--	R	N	--	2	1-2	1-3	2	--	2	R
Sunflower.	1-3	1-3	R	HP	1-3	R	3	HP	3	1-3	3	N
Monarda.	R	--	R	N	3	--	N	1-3	--	--	1-3	--
<i>Plantago</i>	HP	--	--	--	HP	--	3	--	--	1-3	2	1
Common ragweed.	--	Fl	--	--	--	--	--	--	--	--	--	--
Giant Ragweed.	R	HP	St	N	R	R	R	N	N	R	R	R
		Fl	3	HP	N	2	N	HP	Fl	3	R	N
		1-3							Fr			
Crop Plants												
Cotton.	3	R	R	2	N	2	2	1	2	--	1-3	3
Total Eaten.	5	4	4	5	11	10	11	14	9	7	10	7
Total Nibbled and Refused.	10	7	12	10	8	5	8	5	6	6	9	8
Others Refused (Not in table).	18	4	15	13	12	4	7	15	2	8	13	5
Others Eaten (Not in table).	4	--	1	4	6	6	6	21	0	9	14	3
Grand Totals.	37	15	32	32	37	25	32	55	17	30	46	23

one select their host-plants from among the dicotyledons. The major selections were made from among the Compositae. Only two other dicotyledonous families appear in the Table 3 list, Labiateae, represented by *Monarda*, and Plantaginaceae, represented by *Plantago*. The leaves alone are not chosen for food, but several species have a tendency to feed on the flowers and in a few cases on the fruit of flowering plants.

Melanoplus differentialis (Thos.), as one of the chief economic grasshoppers of the central states, has been extensively studied by economic entomologists with reference to its food habits. In our cages *M. differentialis* proved to have a striking preference for crop plants, especially cotton. In cages supplied with cotton, sunflower, giant ragweed, Johnson, and other grasses, *M. differentialis* would defoliate the cotton shoots before giving much attention to other foliage. Our cage records, however, supported by my field observations indicate that *M. differentialis* in its natural environments often feeds upon the coarse grasses and weeds listed above. Although often found roosting on the common ragweed (*Ambrosia psilostachya* DC.), in all of our tests *M. differentialis* refused to eat the leaves and flowers of this plant except when other plants were not available. While it feeds greedily on young corn and wheat, it fed sparingly or not at all on native grasses, *Andropogon* and tall grama grass, supplied in our cages.

Thelesperma trifidum (Poir.) Britton proved to be one of the chief host-plants of *Paraidemona punctata* (Stål). While several species of flowering plants may serve as suitable host-plants for this wingless acridian it is definitely a selective feeder. In the fields optimum numbers are associated with patches of *Thelesperma*, *Gaillardia pulchella* Foug., and *Plantago*. This small yellow grasshopper is widely distributed in north central Texas. In optimum habitats it reaches swarming (Isely 1937, p. 334) numbers during June. While occasional specimens are encountered even in August, large numbers disappear early with the fading of *Thelesperma* and *Gaillardia*. Just how one may misjudge a possible host-plant is shown by my field notes of June 6, 1932. *P. punctata* was swarming in an abandoned "shell rock," marl field overgrown with what appeared to be a pure stand of *Croton monanthogynus* Michx. On this field evidence I assumed that this croton was the host-plant of *P. punctata*. In later cage studies *P. punctata* refused to eat *Croton*.

Campylacantha olivacea olivacea Sc. is of special interest in its selective feeding. *Ambrosia psilostachya* DC., its host-plant, was refused or eaten sparingly by other species tested in our cages. As already indicated in the discussions of Figure 5, *C. o. olivacea* is primarily a flower and fruit feeder.

Two species that have received considerable attention in the matter of their food preferences belong to the genus *Hesperotettix*. Field workers frequently report these two species associated in the same habitat. Field observations and cage testing, however, point to *Amphiachyris dracunculoides* (DC.) Nutt. as the host-plant of *Hesperotettix viridis viridis* (Thos.), and to *Helianthus annuus* L. as the primary host of *Hesperotettix speciosus* (Sc.). In my enclosed experimental garden I observed in the late spring and early summer of 1937 a small colony of *H. speciosus* develop through an entire series of instars in association with a single large sunflower plant. They roosted in the axils of the leaves and on the stems. The fuzzy silver white

juveniles harmonize very well with the woolly white stems of the sunflower.

Melanoplus texanus (Sc.) received a great deal of experimental attention in our food preference studies. While it would eat under starvation pressure the foliage of a number of plants, *Gaillardia pulchella* Foug. and *Plantago* proved to be the choices among the food plants offered. Field checks show that *Gaillardia* communities afford maximum numbers of this common short-winged June acridian.

Melanoplus plebejus (Stål) was the only representative of the sub-family Cyrtacanthacrinae which definitely preferred grasses. This species was not very extensively studied. Its feeding behavior is indicated in the discussion in connection with Figure 5.

Melanoplus flabellatus Sc., a very wide ranging species, undoubtedly has a larger number of suitable host-plants than our cage studies suggest. Tests point to *Engelmannia pinnatifida* T. & G. as one of the possible host-plants of this species.

Melanoplus ponderosus ponderosus Sc. has already been mentioned in connection with Figure 5. This species shows a marked preference for flowers and fruit as food.

Two species that were persistently studied in cages were *Melanoplus confusus* Sc. and *Melanoplus impiger* Sc. The former is a widely distributed spring species but not especially abundant in any given habitat locally. In tests no plant was found which was especially selected as food by this species (Tables 3 & 5). *M. impiger* also gave difficulty for two seasons. Field observations and cage tests in 1937, however, pointed to the *Rudbeckia hirta* L., as the host-plant for this species.

Dactylotum pictum (Thos.), sometimes called the "barber pole grasshopper," is a selective feeder. In field checking it was only found as an occasional specimen unless definitely associated with its primary host-plant, *Baccharis texana* (T. & G.) Gray. In addition to the species shown in Table 3 several other spine-breasted grasshoppers were checked for food preferences for short periods in our cages.

Hypochlora alba (Dodge), as various field workers have suggested, is definitely associated with the white sage, *Artemisia ludoviciana* Nutt., as its specific host-plant. Cage tests show that *H. alba* will, however, live for ten days supplied with broomweed and sunflower.

Melanoplus discolor (Sc.) in cages showed a definite preference for *Salvia farinaceae* Benth. This small short-winged grasshopper has a wide distribution, especially in prairie pastures, and may have other food preferences.

The food preferences of *Melanoplus keeleri keeleri* (Thos.), and *Melanoplus mexicanus mexicanus* (Sauss.), were especially studied by one of my students, Miss Frances Kelly, in the Trinity University Biological Laboratory (1935-1936). Miss Kelly's unpublished paper reports that *M. k.*

keeleri feeds upon several dicotyledons. *Parthenium hysterophorus* L., and giant ragweed (*Ambrosia aptera* DC.), are named as host-plants. *M. m. mexicanus* has been thoroughly studied by economic entomologists. In our cages *M. m. mexicanus* selected rather widely among monocotyledons and dicotyledons showing a definite preference for crop plants.

Melanoplus scudderi latus Morse, a late fall, timber margin species, selected the foliage of the giant ragweed, sunflower, and *Parthenium* as food. Among the crop plants, alfalfa (*Medicago sativa* L.) was eagerly eaten.

ADDITIONAL PLANTS OFFERED AS FOOD

As already indicated the plants listed in Tables 1-3 represent plant species found to be acceptable as food to one or more of the acridian species being checked for food preferences. Furthermore, with the exception of the crop plants these plants belonged to the flora of the habitats from which the acridians were collected.

The plants listed, which follow, are made up chiefly of two different groups of plants, as far as their distribution is concerned. In the first group belong species of plants represented by large numbers of individuals in the flora of optimum habitats of the acridians being studied. These plants, however, were for the most part refused in our cages as food or eaten sparingly. In the second group belong chiefly pest-weeds and pest-grasses found in gardens, fields, and vacant lots. To the second group may be added a few of the common garden and crop plants. The plants of the second group were handy for use as fresh green foods or at times were used as emergency foods when other vegetation from the flora of optimum acridian habitats was not available. The chief interest in the latter group of plants lies in the fact that if eaten they serve to show the adaptability of grasshoppers to plant foods which are not in their regular menu. Group one plants are as follows:

Meriolix spinulosa (T. & G.) Heller; *Megapterium missouriense* (Sims) Spach., Giant Evening Primrose; *Daucus pusillus* Michx., Wild Carrot; *Stillingia sylvatica* L.; *Paronychia scoparia* Small, Whisk-broom; *Verbena bipinnatifida* Nutt., Wild Verbena; *Valerianella amarella* Krok., Geometric chickweed; *Opuntia humifusa* Raf., Cactus; *Penstemon cobaea* Nutt.; *Brauneria angustifolia* (D. C. Heller), Pink Cone Flower.

To the second group belong the following: *Hieracium longipilum* Torr., Wild lettuce; *Linum lewisii* Pursh., Blue Flax; *Lupinus texensis* Hook, Texas Blue-bonnet; *Sonchus asper* (L.) Hill, Sow-thistle; *Oxalis* sp.; *Melilotus alba* Desv., Sweet clover; *Carduus virginiana* L., Common Thistle; *Ratibida columnaris* (Sims) D. Don, Niggerhead. In this plant series wild lettuce and sow-thistle were freely eaten by several acridian species.

Several grasses were eagerly eaten, often in preference to grasses from optimum acridian habitats. Among these grasses were the following: *Poa*

annua L., Annual bluegrass; *Hordeum pusillum* Nutt., Little barley; *Limnoda arkansana* (Nutt.) L. H. Dewey; *Digitaria sanguinalis* (L.) Scop.; *Echinochloa colonum* (L.) Link, Jungle rice.

The repeated selection by grasshoppers of foods not in their normal menu emphasizes the complexity of the environmental factors which control their living conditions. The ever present effectiveness of the law of the minimum (Hesse 1937, p. 21) must serve to limit certain acridians to environments where even preferred foods may not be available. Under these conditions, second choice foods with proper diet prerequisites have become established as host-plants.

In this argument the fact must not be overlooked that plants eaten freely may not always contain the necessary diet requirements for species maintenance (Hodge 1933; Carothers 1923).

STARVATION EXPERIMENTS

Cage studies dealing with the reactions of Acrididae to a wide variety of plant foods clearly demonstrated that at least 30 of the forty species checked should be classed as selective feeders. In other words, the number of palatable food plants for most species was found to be limited. To further examine the current biological as well as layman's theory that grasshoppers "eat everything green" and are both "*polyphagous* and *omnivorous*," a series of unpalatable food experiments was devised. The name starvation experiments has been applied to these tests since it was soon found that many species of grasshoppers would die in the absence of their specific host-plants, even when an abundance of fresh green vegetation, acceptable to other acridian species, was provided in their cages. The routine of these experiments was varied. The details of the tests are briefly summarized in the following paragraphs and tables.

Experiment 1—Two regulation cages (Fig. 1) were used. The food for Cage 1 represented four pasture grasses from the optimum habitats of the grasshopper species being tested:

Andropogon saccharoides Swartz
Stipa leucotricha Trin. and Rupr.
Aristida purpurea Nutt.
Cynodon dactylon (L.) Pers.

The food for Cage 2 was selected from abundant early June forbs also found in the optimum habitats of these species. The following forbs were used:

Gaillardia pulchella Foug.
Plantago sp.
Thelesperma trifidum (Poir.) Britton
Eragrostis multicaulis DC.

On June 3, 1937 thirty specimens of four common June acridians were placed in each of the cages:

	I.		II.	
	Male	Female	Male	Female
<i>Melanoplus confusus</i> Sc.....	4	4	4	4
<i>Melanoplus texanus</i> (Sc.).....	4	4	4	4
<i>Paraidemona punctata</i> (Stål).....	4	4	4	4
<i>Acrolophitus variegatus</i> (Thos.).....	3	3	3	3

TABLE 4. STARVATION EXPERIMENT NO. 1
Longevity of four different acridian species supplied with:
I. Grasses, II. Forbs

Date 1937	Acridian Species	Cage 1. Grasses Numbers			Cage 2. Forbs Numbers		
		Male	Female	Dead	Male	Female	Dead
June 3	<i>M. confusus</i>	4	4	0	4	4	0
	<i>M. texanus</i>	4	4	0	4	4	0
	<i>P. punctata</i>	4	4	0	4	4	0
	<i>A. variegatus</i>	3	3	0	3	3	0
June 5	<i>M. confusus</i>	4	4	0	3	4	1
	<i>M. texanus</i>	2	4	2	4	4	0
	<i>P. punctata</i>	1	2	5	4	3	1
	<i>A. variegatus</i>	1	2	3	3	2	1
June 8	<i>M. confusus</i>	3	2	2	2	3	2
	<i>M. texanus</i>	1	4	1	4	3	1
	<i>P. punctata</i>	0	1	2	4	3	0
	<i>A. variegatus</i>	0	1	2	3	2	0
June 12	<i>M. confusus</i>	0	1	5	1	1	3
	<i>M. texanus</i>	0	2	3	3	3	1
	<i>P. punctata</i>	0	0	1	4	3	0
	<i>A. variegatus</i>	0	0	1	3	2	0
June 16	<i>M. confusus</i>	0	0	1	1	1	0
	<i>M. texanus</i>	0	0	2	3	3	0
	<i>P. punctata</i>	0	0	0	4	2	1
	<i>A. variegatus</i>	0	0	0	3	2	0
	Totals.....	All dead.....30			19 Alive		11 Dead

The results in Table 4 are positive. In Cage 1 the thirty acridians belonging to four different species were supplied daily with fresh grasses representing three of the dominant native grasses of the grand prairies and naturalized Bermuda grass. The record shows that at the close of the ninth day twenty-seven specimens were dead in Cage 1 and only three individuals remained. At the close of the thirteenth day the last three Cage 1 grasshoppers died. It is obvious that these species starved with a fresh supply of green grass as food.

In Cage 2 the acridians were supplied with forbs. In the case of three species the forbs used had been designated in Tables 1-3 as their host-plants.

In the case of *Melanoplus confusus* a specific host-plant had not been fully determined. At the close of the thirteenth day, eleven of the Cage 2 specimens were dead. Six of these belonged to the species *Melanoplus confusus*.

Experiment 2—The acridian species used in this test were chiefly grass feeders. (See Tables 1-3). When available only males were used. In several cases the full number of males was not available, and females were substituted. *Melanoplus differentialis* (Thos.) was introduced into this series for possible comparative data that might come from a study of its feeding behavior in association with the grass feeders. The foods for Cage 1 were three grasses:

- Andropogon saccharoides* Swartz—(Beard grass)
- Sporobolus heterolepis* A. Gray—(Dropseed)
- Sorghum halepense* (L.) Pers.—(Johnson grass).

In Cage 2 only forbs were supplied as food. These were selected from among the host-plants of other August acridians (Table 6). These broad-leaved flowering plants were to be found in the fields as mixed weeds along with the grasses used in Cage 1. The forbs used in Cage 2 were as follows:

- Amphiachyris dracunculoides* (DC.) Nutt.—(Broomweed)
- Ambrosia psilostachya* DC.—(Common ragweed)
- Houstonia angustifolia* Michx.—(Houstonia)
- Artemisia ludoviciana* Nutt.—(White sage)

The *Houstonia* was used in the tests for the first two days. After that white sage was substituted.

This is one of the most spectacular experiments of the entire series. The results are so striking that comment is hardly necessary.

The first three species listed in Cage 2, Table 5, are exclusive grass feeders and all Acridinae. The record shows that these succumb quickly in the absence of grasses from their menu. Several specimens of *Chortophaga viridifasciata* and *Encoptolopus sordidus costalis* survived a few days longer, but these also starved in the presence of an abundance of fresh dicotyledonous food. At the close of the first week only nine specimens remained alive in Cage 2. Five of the nine belong to the species *Melanoplus differentialis* and three to *Geneotettix deorum*. The record of this experiment seems to suggest that *G. deorum* does not depend wholly on grasses for its diet. The versatility and adaptability of *M. differentialis* to maintain itself on plant foods not belonging to its first choices are noteworthy. All ten specimens of *M. differentialis* in Cages 1 and 2, (Table 5) were alive and apparently in good physical condition at the close of the experiment, September 1, eight days after its beginning. This marked adaptability of this pest species may largely explain its destructive propensities.

The Cage 1 record is self-explanatory. All the grass feeders show a good average vitality with a fresh supply of their grass diet available.

TABLE 5. STARVATION EXPERIMENT NO. 2

Longevity of grass feeders when supplied with a variety of forbs from among the host-plants of other acridians. The pest grasshopper, *M. differentialis*, represents a polyphagous species

Date 1937	Acridian Species	Cage 1. Grasses Numbers		Cage 2. Forbs Numbers	
		Alive	Dead	Alive	Dead
August 23	<i>S. admirabilis</i>	5	0	5	0
	<i>M. maculipennis</i>	5	0	5	0
	<i>M. neomexicana</i>	5	0	5	0
	<i>C. viridifasciata</i>	5	0	5	0
	<i>E. s. costalis</i>	5	0	5	0
	<i>G. deorum</i>	5	0	5	0
	<i>M. differentialis</i>	5	0	5	0
August 25	<i>S. admirabilis</i>	5	0	3	2
	<i>M. maculipennis</i>	4	1	1	4
	<i>M. neomexicana</i>	5	0	4	1
	<i>C. viridifasciata</i>	5	0	5	0
	<i>E. s. costalis</i>	5	0	5	0
	<i>G. deorum</i>	5	0	4	1
	<i>M. differentialis</i>	5	0	5	0
August 26	<i>S. admirabilis</i>	5	0	0	5
	<i>M. maculipennis</i>	4	0	0	4
	<i>M. neomexicana</i>	4	1	0	5
	<i>C. viridifasciata</i>	5	0	3	2
	<i>E. s. costalis</i>	5	0	5	0
	<i>G. deorum</i>	4	1	3	2
	<i>M. differentialis</i>	5	0	5	0
August 28	<i>S. admirabilis</i>	5	0	0	0
	<i>M. maculipennis</i>	4	0	0	0
	<i>M. neomexicana</i>	4	0	0	0
	<i>C. viridifasciata</i>	5	0	2	1
	<i>E. s. costalis</i>	5	0	3	2
	<i>G. deorum</i>	4	0	3	0
	<i>M. differentialis</i>	5	0	5	0
August 30	<i>S. admirabilis</i>	5	0	0	0
	<i>M. maculipennis</i>	4	0	0	0
	<i>M. neomexicana</i>	4	0	0	0
	<i>C. viridifasciata</i>	5	0	0	0
	<i>E. s. costalis</i>	5	0	1	2
	<i>G. deorum</i>	4	0	3	0
	<i>M. differentialis</i>	5	0	5	0
September 1	<i>S. admirabilis</i>	4	1	0	0
	<i>M. maculipennis</i>	4	0	0	0
	<i>M. neomexicana</i>	4	0	0	0
	<i>C. viridifasciata</i>	5	0	0	0
	<i>E. s. costalis</i>	5	0	0	1
	<i>G. deorum</i>	4	0	3	0
	<i>M. differentialis</i>	5	0	5	0
	Totals	31 Alive	4 Dead	8 Alive	27 Dead

The results of Experiments 1 and 2, Tables 4 and 5, *should explode the dictum that grasshoppers "eat everything green."* It is evident that nine of

the eleven species tested in these experiments will starve in the presence of abundant vegetation representing host-plant selections of other acridian species. It is noteworthy that this list of nine contains representative species from all three of the major North American sub-families of the Acrididae.

Experiment 3—The acridian species used in Experiment 3 feed chiefly on broad-leaved plants. Eight species were used:

Hesperotettix viridis viridis (Thos.)
Hesperotettix viridis pratensis (Sc.)
Hesperotettix speciosus (Sc.)
Melanoplus plebejus (Stål)

Hypochlora alba (Dodge)
Campylacantha olivacea olivacea Sc.
Trimerotropis pistrinaria Sauss.
Hadrotettix trifasciatus (Say)

At first only two cages were arranged. Forty specimens, five individuals of each species were put in each cage. The plant materials in Cage 1 were arranged as follows:

<i>Amphiachyris dracunculoides</i> (DC.) Nutt.....	Broomweed
<i>Solidago petiolaris</i> Ait.....	Goldenrod
<i>Helianthus annuus</i>	Sunflower
<i>Andropogon saccharoides</i> Swartz.....	Beard grass

In Cage 2 the following plants were supplied:

<i>Artemisia ludoviciana</i> Nutt.....	White Sage
<i>Ambrosia psilostachya</i> DC.....	Common Ragweed
<i>Hymenopappus corymbosus</i> T. & G.....	Hymenopappus
<i>Asclepiodora decumbens</i> (Nutt.) A. Gray.....	Milkweed

The plants in Cage 1 consisted of the host-plants of the first four species of acridians. The Cage 2 plants consisted of the host-plants of the last four species. Six of the plants used are shown in Table 3 as the first choices of the species concerned. *H. v. pratensis* was not among the species shown in Table 3. Its host-plant, however, *Solidago petiolaris* Ait., was among the food plants in Cage 1. In the case of *M. plebejus*, instead of Johnson grass beard grass was supplied.

Experiment 3 was started on August 23. On August 28 it was decided to introduce a third cage using forty specimens belonging to the same species as in Cages 1 and 2. Cage 3 was to be supplied with grasses for food but no forbs. The grasses selected were acceptable food plants for the grass feeders tested in Experiment 2, Table 5. The grasses supplied were as follows:

Andropogon saccharoides Swartz—Beard Grass
Sorghum halepense (L.) Pers.—Johnson Grass
Sporobolus heterolepis A. Gray—Dropseed

On September 1 we replaced the Johnson grass with
Andropogon furcatus Muhl—Bluejoint Turkeyfoot.

The results of this experiment are shown in Table 6.

TABLE 6. STARVATION EXPERIMENT NO. 3
Adaptability of Eight Acridian Species to Three Different Plant Menus

Date 1937	Acridian Species	Cage 1. Host-plants of H.v.v., H.p., H.s. and M.p. Numbers		Cage 2. Host-plants of H.a., C.o.o., T.p. and H.t. Numbers		Cage 3. Host-plants of grass feeders, Cage 1, Exp. 2. Numbers	
		Alive	Dead	Alive	Dead	Alive	Dead
Aug. 23	<i>H. viridis</i>	5	0	5	0	Not started	
	<i>H. pratensis</i>	5	0	5	0		
	<i>H. speciosus</i>	5	0	5	0		
	<i>M. plebejus</i>	5	0	5	0		
	<i>H. alba</i>	5	0	5	0		
	<i>C. olivacea</i>	5	0	5	0		
	<i>T. pistrinaria</i>	5	0	5	0		
	<i>H. trifasciatus</i>	5	0	5	0		
Aug. 25	<i>H. viridis</i>	5	0	4	1	Not started	
	<i>H. pratensis</i>	5	0	3	2		
	<i>H. speciosus</i>	5	0	4	1		
	<i>M. plebejus</i>	5	0	4	1		
	<i>H. alba</i>	5	0	4	1		
	<i>C. olivacea</i>	4	1	4	1		
	<i>T. pistrinaria</i>	3	2	4	1	Started Aug. 28	
	<i>H. trifasciatus</i>	4	1	5	0		
Aug. 27	<i>H. viridis</i>	5	0	2	2	5	0
	<i>H. pratensis</i>	5	0	0	3	5	0
	<i>H. speciosus</i>	5	0	0	3	5	0
	<i>M. plebejus</i>	5	0	4	0	5	0
	<i>H. alba</i>	5	0	4	0	5	0
	<i>C. olivacea</i>	4	0	4	0	5	0
	<i>T. pistrinaria</i>	1	2	4	0	5	0
	<i>H. trifasciatus</i>	2	2	4	1	5	0
Aug. 30	<i>H. viridis</i>	5	0	1	1	5	0
	<i>H. pratensis</i>	5	0	0	0	1	4
	<i>H. speciosus</i>	5	0	4	0	3	2
	<i>M. plebejus</i>	5	0	4	0	5	0
	<i>H. alba</i>	4	1	4	0	5	0
	<i>C. olivacea</i>	2	2	4	0	3	2
	<i>T. pistrinaria</i>	0	1	3	1	5	0
	<i>H. trifasciatus</i>	1	1	3	1	5	0
Sept. 1	<i>H. viridis</i>	5	0	0	1	5	0
	<i>H. pratensis</i>	5	0	0	0	1	0
	<i>H. speciosus</i>	5	0	4	0	2	1
	<i>M. plebejus</i>	5	0	4	0	5	0
	<i>H. alba</i>	1	1	4	0	3	2
	<i>C. olivacea</i>	2	0	4	0	3	0
	<i>T. pistrinaria</i>	0	0	3	0	5	0
	<i>H. trifasciatus</i>	0	1	4	0	4	1
Sept. 3	<i>H. viridis</i>	5	0	0	0	0	5
	<i>H. pratensis</i>	5	0	0	0	0	1
	<i>H. speciosus</i>	5	0	4	0	0	2
	<i>M. plebejus</i>	5	0	4	0	4	1
	<i>H. alba</i>	0	1	4	0	3	0
	<i>C. olivacea</i>	3	0	4	0	0	3
	<i>T. pistrinaria</i>	0	0	3	0	5	0
	<i>H. trifasciatus</i>	0	0	4	0	3	1
Totals.		Alive	Dead	Alive	Dead	Alive	Dead
	Upper 4 species	20	0	8	12	4	16
	Lower 4 species	3	17	15	5	11	9

Cages 1 and 2 were closed out September 3. Cage 3 was continued until September 10. At that time there were still five live grasshoppers in Cage 3. These were: *H. trifasciatus* 3, *T. pistrinaria* 1, and *M. plebejus* 1. It was evident that even these survivors were not thriving on the prairie grass menus supplied in Cage 3.

The results of Experiment 3 are shown in the totals of Table 6. In Cage 1 all the grasshoppers belonging to the upper four of the eight species being tested were alive. These had been supplied with their host-plants as food. Only three grasshoppers belonging to the lower four species were alive in Cage 1.

In Cage 2 the results were not quite as definite. Fifteen grasshoppers were alive to represent the lower four species and four each of *H. speciosus* and *M. plebejus*. Cage 3 results, however, show that even *H. speciosus* and *M. plebejus* have specific food requirements.

In Experiment 3 the same facts stand out which were apparent in Experiments 1 and 2, Tables 4 and 5. Many species of grasshoppers are selective feeders and will soon die in the presence of abundant fresh vegetation if they are deprived of their host-plants. The case of *Campylacantha olivacea olivacea* is cleared up if we compare Table 3 and Figure 5. While the chief food of this species is made up of the foliage of the common rag-weed their feeding on the flowers of *Amphiachyris* explains their longevity in this experiment. The hardiness of *Hypochlora alba* came as a surprise. *Melanoplus plebejus* and *Hesperotettix speciosus* in Cages 1 and 2 are evidently more adaptable to the forbs foods supplied than are the other species. In Cage 3, however, with a grass diet a zero is found in the alive column for *H. speciosus* at the close of the tenth day. In Cage 3 *Trimerotropis pistrinaria* stands out as having five survivors on the sixth day with a grass diet. Fasting tests show, however, that even in warm weather certain species from xeric habitats will live without food or water for a week. Mature females usually live longer than males in starvation tests.

STARVATION IN ABSENCE OF FOOD

Under normal north central Texas summer temperatures and the consequent high metabolism, how long can a grasshopper live without food? There are, no doubt, individual differences as well as species differences. In order to make a further trial a no-food experiment was set up on September 1, 1937.

Vigorous pairs of all of the fifteen species used in Experiments 2 and 3 (Table 5 and 6) were placed in a cage (Fig. 1) without food. In addition to these, pairs of the following species were added: *Melanoplus discolor* (Sc.), *M. k. keeleri* (Thos.), *M. bispinosus* Sc., and *M. p. ponderosus* Sc., making 19 pairs or 38 specimens in all. The empty soil pans were filled with clean sand; water was supplied daily by wetting the sand and the sides of the cage. The temperature during the period the experiment was in progress, September 1-10, ranged from a minimum of 68°F to a maximum of

96°F. All daily maximum records for the period were between 92°-96°F. Minimum night temperatures were between 68°-74°F.

On September 3, two days after the experiment started, 9 specimens were dead; 6 males and 3 females. The dead specimens were always removed as rapidly as seen, for it is well known that grasshoppers will frequently feed on dead ones. However, I have not observed predacious behavior on the part of acridians, although starving grasshoppers will eat off the antennae of those that are dying or nearly dead.

Specimens of other species died gradually until on September 8, after one week in the "no-food" cage, 8 live grasshoppers remained. The species and sexes were as follows: females, one each, *H. trifasciatus*, *H. v. viridis*, and *Hypochlora alba*; one male, *M. differentialis*. For two species, *M. bispinosus* and *M. p. ponderosus*, both males and females were still alive. With the exception of the pair of *M. p. ponderosus* the remaining specimens were dead by September 9. This hardy species in repeated tests lived from 12 to 14 days in cages supplied with water but no food.

In experiments where grasshoppers were supplied with unpalatable food in the cages, as well as in this experiment without food, the absence of feces is noticeable. From the taxonomic viewpoint longevity without food or with unpalatable food shows that the Cyrtacanthacrinae have the greatest powers of survival. The Oedipodinae are second, and the Acridinae are the least hardy among the sub-families studied.

OMNIVOROUS FEEDERS

The idea that grasshoppers are to an extent omnivorous feeders is supported in part by the fact that dead grasshoppers were often eaten in cages. As I have already indicated, acridians show no marked predacious tendencies. In cages where there are many specimens, dead grasshoppers are usually partly eaten even when there is an abundance of palatable food. From the data at hand in these starvation tests, however, this tendency to feed upon dead grasshoppers appears to be of significance only in the temporary maintenance of starvation survivors at times of food shortage until more desirable food is found.

FOOD PREFERENCES ANALYZED

An analysis of the feeding behavior of the forty acridian species experimentally tested shows that exactly twenty of the forty species were primarily grass feeders. The twenty other species chose their host-plants from among the forbs or the broad-leaved flowering plants. These food preferences grouped by acridian sub-families are as follows:

Sub-Family	Grasses	Forbs
Acridinae	9	1
Oedipodinae	10	2
Batrachotetriginae	0	1
Cyrtacanthacrinae	1	16
Totals.....	20	20

Grass eaters, while definitely restricted to grasses, selected their food as a rule rather freely from among several species when these were available.¹⁵ However, certain of the grass species were not acceptable even to the grass eating grasshoppers.

The species showing marked preferences for forbs belong chiefly to the Cyrtacanthacrinae (spine-breasted grasshoppers). Nine of the sixteen species of the Cyrtacanthacrinae selected their food from among the Compositae. This fact is of interest from the evolutionary and taxonomic viewpoints when it is noted that what is believed to be the most recent sub-family phylogenetically selects its host-plants from among the most recent phylogenetic family of the angiosperms.

Cage tests clearly show a correlation among the grass feeders with grass habits of growth. This correlation suggests shelter and protection going hand in hand with plants needed for food. The slender bodied Mermiriae and Syrbulae: *Mermiria maculipennis maculipennis* Bruner, *M. bivittata* (Serville), *M. neomexicana* (Thos.), *Syrbula admirabilis* Uhler, and *S. fuscovittata* (Thos.) find their habitats among the Andropogons, Sporobolus, and the tall grama grasses. *Geneotettix deorum* (Sc.), *Mesochloa abortiva* Bruner, *Opeia obscura* (Thos.), *Orphulella speciosa* (Sc.), and *Trachyrhachis kiowa fuscifrons* (Stål), small, usually somewhat flattened acridians frequent low, mat-like grasses, especially buffalo and Bermuda grass.

East and north certain of these short grass species will be found associated with the blue grasses (Poas). *Chortophaga viridifasciata* (DeGeer), *Arphia simplex* Sc., *Encoptolophus sordidus costalis* (Sc.), and *Dichromorpha viridis* (Sc.) are more frequently associated with the lush grasses of the streams and timber margins.

There are few acridians that are so closely associated with their host-plants as to be found exclusively on a single plant species in field observations. This association involves the use of plants not only as food but for roosting among the shoots and on the branches. *Hypochloa alba* (Dodge), well known to all field students of grasshoppers of the great plains, illustrates in a striking way this behavior in its close association with *Artemisia ludoviciana* Nutt. As far as my field studies are concerned, I have never taken *H. alba* except in the immediate vicinity of its host-plant. In cage tests, however, under starvation pressure it fed on other plants. While not as highly selective and as clean-cut in their natural habitat relationships as *H. alba*, I have found very similar host-plant relationship on the part of *Dactylotum pictum* (Thos.), *Hesperotettix speciosus* (Sc.), *Hesperotettix viridis viridis* (Thos.), *Hesperotettix viridis pratensis* (Sc.), and *Campylacantha olivacea olivacea* Sc. These roost upon and feed upon the foliage

¹⁵ Criddle (1933 a, p. 480) in his study of food preferences of Manitoba grasshoppers found three species, *Opeia obscura* Thos., *Metator pardelinus* Sauss., *Melanoplus o. occidentalis* Thos., selecting *Agropyron smithii* Rydb. as their host-plant. One of these species, *Opeia obscura* Thos., is occasionally represented in the acridian fauna (Isely 1935, p. 43) of north central Texas.

and in some cases the flowers and fruits of the host-plants. Among the Acridinae *Acrolophitus variegatus* (Thos.) is restricted to a specific host-plant, *Evax multicaulis* DC. Certain other species while definitely selecting certain specific plants for food differ in their roosting behavior. These species move about more freely and do not cling as tenaciously to their host-plants. In this list are *Paraidemona punctata* (Stål), *Melanoplus texanus* (Sc.), and *Brachystola magna* (Girard). These species do not mark out their host-plants as definitely as the acridians noted above. When not feeding they are as likely to be found on the ground or other low vegetation as upon their host-plants. Still other species like *Melanoplus differentialis* (Thos.) and *Melanoplus ponderosus ponderosus* Sc. roost frequently upon plants that are not used for food.

Accidental association of acridians and plants have often led field observers to suspect host-plant relationships. Cage studies, however, definitely show that roosting preferences often have no relation to food preferences. For example cage studies show that certain grass feeders (*Syrbula admirabilis* Uhler) roosting on the common ragweed (*Ambrosia psilostachya* DC.) starve if forced to use this plant as food.

The results of the starvation experiments summarized in Tables 4-6 are obvious. Since specific plant species are essential as food for certain acridians. An optimum acridian habitat must be favorable not only to the acridian species but also to the host-plant species.

The seasonal passing of a plant species, the dying of certain plants on account of drouth, or over-grazing in certain pastures will be followed immediately by the dying of the acridian species using these plants for food. Frequently, in a nearby pasture under conditions more favorable to the host-plants, the acridians will continue to thrive, although they have disappeared in the other areas as indicated above. The temporary change under starvation pressure to other plants for food may occur, but for optimum nutrition and reproductive needs the right kind of food is of primary importance. This necessary diet requirement can only be satisfied where specific plants are a part of the flora of the habitat of the acridian species. These facts are further emphasized by the researches of Carothers, Criddle, and Hodges previously cited.

Finally, these food preference and starvation studies indicate that 30 of the 40 species studied are essentially oligophagous. Four species approach monophagy, only two are typically polyphagous. The four species that come the nearest to monophagy in their field behavior are *H. alba*, *D. pictum*, *A. variegatus*, and *H. v. viridis*. To the four may be added *H. v. pratensis*, not included in the forty listed in connection with the tables. The feeding behavior under natural conditions of *H. v. pratensis* is different from the feeding behavior of *H. v. viridis*. In cages *H. v. pratensis* fed on broom-weed, the chief host-plant in our area of *H. v. viridis*. In field checking,

however, it was found that *H. v. pratensis* is closely associated with *Solidago petiolaris* Ait. Further study may place a few of the 30 oligophagous species in the polyphagous group. In the main, however, it may be emphasized that my experiments indicate that north central Texas acridians in general require specific foods for their species maintenance.

SOIL CHOICES FOR OVIPOSITION

SOIL RELATIONS

In the literature at hand¹⁶ I find only two references suggesting experimental study of soil choices for oviposition. McClung (1899, p. 21) made such a test with *Melanoplus differentialis* (Thos.). His results show selective behavior on the part of this species. Uvarov (1928, p. 57) suggests the use of "special cages each containing several different samples of soil."

In a recent paper Shotwell (1935, p. 486) gives descriptions of egg laying sites as usually selected in nature by a few of the best known economic species. Criddle (1918; 1933a, p. 482) has observed and described the egg laying behavior in the field of several Manitoba species. He discusses soil choices for egg laying under natural conditions.

Economic entomologists in describing egg laying sites of pest species usually emphasize the importance of unplowed field margins, fence rows, road sites, and waste fields (soil structure) as possible concentration areas for egg laying. Topography as related to drainage is considered significant. Vegetation affording roots and grass crowns is also pointed out as attracting certain species in selecting sites for egg laying.

That there is a clean-cut correlation between grasshoppers and different soils appears to be the general conclusion of critical field students of these insects. In a recent paper (Isely 1937, p. 325) attention is called to the close interrelations of acridians and soils.

Is this definite association primary and determined by the reactions of acridians to soil structure, texture, moisture, pH, or some other soil factors; or is it secondary and determined by the presence of plants necessary in diet, which are in turn definitely soil related? Certain species, *Spharagemon collare cristatum* (Sc.) and *Melanoplus impiger* Sc., reach their greatest numbers only in light sandy soil habitats. A few other well known examples are: alluvial soil species, *Melanoplus differentialis* (Thos.), and *Dissosteira carolina* (L.); eroded soil species, *Trimacrotropis pistrinaria* Sauss.; calcareous soil species, *Xanthippus corallipes pantherinus* (Sc.).

Dissosteira carolina (L.) in north central Texas is definitely an alluvial soil grasshopper, never abundant but usually found in "first bottom" habitats. In Kansas (Sedgwick County) on account of its distribution the name "road duster" is generally applied to the Carolina grasshopper. In Colorado from 6000-8000 feet elevation (Boulder County) the abundance of *Dis-*

¹⁶ There probably have been other experiments, but in the literature at hand this is the only reference given.

sosteira carolina (L.) is limited to miniature valleys among the rugged mountains. This highly adaptive species appears to vary its choice of habitat, although in the cases cited above wash soils are evidently selected for oviposition.

SOIL SELECTION EXPERIMENTS

The experimental set-up for our food preference testing gave fairly satisfactory results. To secure positive experimental data concerning soil choices for oviposition has proven thus far to be more difficult. Enough data have been secured, however, to emphasize the fact that Acrididae do react to soil differences and appear at times to choose certain types of soil for oviposition in preference to others.

Four hundred and nine egg pods were deposited by thirty-two different acridian species in soil pans in cages. The soils selected for oviposition by eighteen species depositing as many as six pods or more are shown in Table 7. A record of six pods may be suggestive of possible behavior but provides insufficient data for any final deductions.

Further facts concerning egg pods, egg packets, stoppers, and eggs are given in Table 9. The soil pans described in connection with Figure 1 were especially devised to test out acridian soil choices in oviposition. A diagram (Fig. 6) of the floor plan of the cage and the spaces occupied by the soil pans will help to explain the technique used in testing reactions of Acrididae to soils for egg laying.

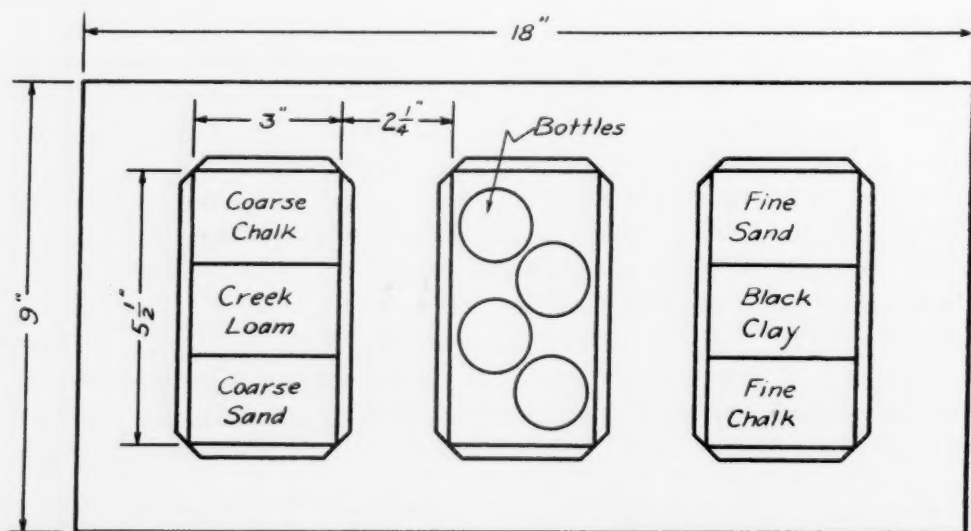


FIG. 6. A diagram of a cage floor (Fig. 1) showing soil compartments used for checking soil choices for oviposition. Five or six different kinds of soils were usually available. The female grasshoppers, after testing, selected from among these soils the particular sites for depositing their egg pods. Turf was sometimes substituted for one of the other soils. The bottles in the center soil pans were used to hold fresh plant shoots for food. Fig. 1 shows soil pans on top of the cage. Compartments and soils in these pans are also shown.

The different soils were secured from optimum habitats of the various species to be tested. Some of the common local soil types used were the following: (1) chalk or marl, the eroded sub-soils of Houston clay shallow phase areas; (2) creek loam, alluvial soils, a mixture of water-lain soils, silt and sand; (3) black clay soils representing the stiff Houston clay of the blackland prairies; (4) fine sand secured from the east Texas timbers or the Cahaba fine sands; (5) coarse sand; (6) sifted chalk or marl; (7) turf, small blocks or transplanted turf. Soil 6 was a fine grained calcareous soil with a structure similar to "fine sand" in 4. Soils 5 and 1 were also similar in structure, although very different in texture. Soils 6 and 7 were introduced late in this series of experiments and were not placed in the cages in the earlier tests which were used to check the reactions of grasshoppers to soils differing in texture, structure, and chemical composition. Soils 1-6 were bare soils and without vegetation. After various soils were placed in the several compartments of the soil pans they were thoroughly settled by wetting. The turf blocks of soil employed in a few of the experiments gave opportunity for selection of oviposition sites associated with vegetation.

ACRIDIAN SPECIES USED FOR OVIPOSITION EXPERIMENTS

Mature females secured directly from optimum habitats were used for oviposition experiments. As a rule from twenty to forty specimens, males and females in approximately equal numbers, were placed in a cage (Fig. 1). These cages were usually arranged with five or six different kinds of soils in the compartments of the soil boxes. The third soil pan was used to hold plant materials for food, and frequently one of the six smaller compartments was also used to hold plant materials. In addition the floor on the sides of the cage (Fig. 1) was used for bottles to hold food materials. When the host-plants were known these, if available, were always supplied for food. It was found that the right kind of food is of primary importance in securing egg laying activity.

Since all of the species studied in Tables 7 and 9 have been listed with their full scientific names in connection with Tables 1-3, this detailed list is not repeated in connection with these tables.

A study of Table 7 suggests that many of the species tested preferred soils made up of fine particles for egg laying. It is noteworthy that after the sifted-chalk-marl was introduced (FiCh), that with one exception, this fine structured calcareous marl paralleled rather closely the fine arenaceous sand

¹⁷ These soils are described in county and state soil surveys (Isely 1937, p. 321). Soil texture is best indicated by mechanical analysis.

Mechanical Analysis of Ellis County Soils as given by Bennett 1911, Soil Survey of Ellis County, Texas, U. S. Bur. Soils, 1-34

Type of Soil	Fine Gravel Per cent	Coarse Sand Per cent	Medium Sand Per cent	Fine Sand Per cent	Very fine Sand Per cent	Silt Per cent	Clay Per cent
Houston Black Clay.....	0.4	1.4	0.8	3.0	7.6	44.7	42.2
Houston Stony Clay.....	0.0	0.4	0.4	4.9	26.2	44.1	24.4
Trinity Clay	0.1	0.5	1.3	4.4	2.3	29.4	60.1
Bienville Fine Sand.....	0.0	1.0	12.3	76.4	5.0	2.7	2.5

TABLE 7. SOILS CHOSEN FOR OVIPOSITION

COLUMN HEADINGS:

Dates —Duration of tests.
I-XII —Months.
AvF —Average number females in cage.
Total Pods —Total egg pods.

SOILS:

CoCh —Coarse Chalk or Marl.
CrLm —Creek Loam.

CoSd —Coarse Sand.
BlCl —Black Clay.
FiSd —Fine Sand.
FiCh —Sifted Fine Chalk.
Tf —Turf.
O-21 —Number of pods.
— —Not used.

Arrangement of species in seasonal sequence of acridian egg laying
Number of Egg Pods Laid in Different Soils

Acridian Species	Dates 1936	AvF	CoCh	CrLm	CoSd	BlCl	FiSd	FiCh	Tf	Total Pods
<i>M. confusus</i>	V,4-31.....	24	3	9	5	4	16	--	--	37
<i>A. simplex</i>	VI,1-20.....	24	6	15	5	8	13	--	--	47
<i>X. c. pantherinus</i>	VI,1-VII,11.....	11	1	0	4	2	7	1	0	15
<i>P. punctata</i>	VI,1-22.....	40	13	8	21	3	18	--	--	63
<i>M. texanus</i>	VI,1-25.....	20	2	12	4	3	13	--	0	34
<i>P. saussurei</i>	VI,15-VII,18.....	10	0	1	1	0	4	2	0	8
<i>S. c. cristatum</i>	VI,20-30.....	19	0	3	1	0	7	5	--	16
<i>H. v. viridis</i>	VII,1-31.....	28	7	0	5	1	2	0	17	32
<i>H. speciosus</i>	VII,1-31.....	22	10	3	5	2	4	16	--	40
<i>M. flabellatus</i>	VII,1-16.....	6	2	1	4	1	0	0	--	8
<i>D. pictum</i>	VII,13-VIII,3.....	15	2	4	1	1	3	0	--	11
<i>H. trifasciatus</i>	VII,29-VIII,5.....	15	2	0	3	--	1	0	0	6
<i>M. discolor</i>	VIII,1-8.....	30	0	5	0	--	5	4	--	14
<i>G. deorum</i>	VIII,1-8.....	11	0	0	0	0	9	0	0	9
<i>C. o. olivacea</i>	IX,20-30.....	10	0	1	0	0	3	4	0	8
<i>S. admirabilis</i>	XI,1-28.....	6	0	4	0	0	3	0	--	7
<i>M. k. keeleri</i>	XI,1-30.....	10	0	2	0	5	15	2	--	24
<i>M. m. mexicanus</i>	XI,27-XII,4.....	4	--	--	--	3	3	3	--	9
Totals.....			48	68	59	33	126	37	17	388

in the number of times it was selected for oviposition. Four species (*S. c. cristatum*, *M. discolor*, *C. o. olivacea* and *M. m. mexicanus*) show this similarity in their reactions to soil structure and apparently disregard differences in the chemical composition of soils.

Soils made up of *fine particles* composed of fine sand, sifted-chalk-marl, and creek loam were selected for egg laying sites in preference to soils of *coarse materials* made up of gravel, broken rock, and stiff clay. These fine structured soils were chosen for egg laying sites in preference to the coarse structured soils in cage tests as follows:

Spharagemon collare cristatum (Sc.) selected soils made up of five particles for the laying of 16 pods out of a total of 17 egg pods, *Pardalophora saussurei* (Sc.) 7 times out of 8, *Geneotettix deorum* (Sc.) 9 times out of 9, *Melanoplus discolor* (Sc.) 14 times out of 14, *Melanoplus keeleri keeleri* (Thos.) 17 times out of 24, *Melanoplus confusus* Sc. 25 times out of 38, *Arphia simplex* Sc. 28 times out of 47, *Campylacantha olivacea olivacea* Sc. 7 times out of 8, *Syrbula admirabilis* Uhler 7 times out of 7.

For the nine species listed above these tests show that out of 172 egg pods deposited 130 were placed in soils made up of fine particles to 42 laid in soils made up chiefly of coarse materials or a ratio of 3 to 1 in favor of

soils composed of fine particles. Other reactions may be studied in Tables 7 and 8.

In comparison with these fairly uniform reactions to soil differences *Paraidemona punctata* (Stål) selected coarse structured soils 34 times in laying a total of 64 pods. *Hesperotettix speciosus* (Sc.) is of interest in selecting calcareous soils 26 times out of a total of 40 pods laid. *H. v. viridis* (Thos.) was the only species to select turf.

Herbert Knutson (1937), using a set-up similar to the ones summarized in Table 7, reports some interesting egg laying reactions for *Encoptolophus sordidis costalis* (Sc.). The black soil used by Knutson was secured from an optimum habitat of *E. s. costalis* and in terms of my classification would be similar to the black clay known to north central Texas soil students as Houston black waxy-clay. His experiments were carried on in the Biology Laboratory of Southern Methodist University and were continued for several months (October-May, 1936-1937). In the soil pans in his cages Knutson secured 204 egg pods of *E. s. costalis*. The data given in his thesis are as follows:¹⁸

Type of Soil	Number of Eggs Pods Found ¹	Percentage of Total Pods Laid
Black	111	54.4%
Limestone	44	21.5%
Sand	20	9.8%
Red Sand	18	8.8%
Gravel	11	5.4%

In this study *E. s. costalis* selected calcareous soil 155 times in depositing 204 egg pods—a percentage of 75.9% of total pods laid.

In Figure 7 and Table 9 a few facts are given concerning egg pods and eggs. The female grasshopper first forms a cavity in the soil with her ovipositors in which the egg pod is deposited. These egg pods vary in size and form. As a rule, they correspond in size in a general way with the size of the grasshopper. As shown in Figure 7 the extremes in the size of the pods are represented by the large egg sacs of *Brachystola magna* (Girard) and *Pardalophora saussurei* (Sc.) on the one hand and the small egg pods of *Melanoplus flabellatus* Sc. and *Geneotettix deorum* (Sc.) on the other. The entire egg pod is usually made up of two parts, the egg packet proper and the stopper, a plug of mucilaginous material. In certain species *Hesperotettix viridis viridis* (Thos.) and *Hesperotettix speciosus* (Sc.), the stopper is represented by a thin layer of frothy material. In other cases, as *Spharagemon collare cristatum* (Sc.), the stopper represents four-fifths of the entire length of the pod. In Table 9 the average lengths of typical pods are indicated, as well as the relative lengths of the egg packet or mass of eggs as compared with the length of the stopper. The figures given for the average number of eggs in a packet represent the average number

¹⁸ Mr. Knutson has kindly given permission to use his thesis data (unpublished). His cages (Fig. 1) and soil pans were the same as those used in the writer's experiments.

actually counted. The size of the eggs is surprisingly uniform. Measurements suggest 5 mm. as the average length of the eggs of many of the species studied. The eggs of the wingless species, *Paraidemona punctata* (Stål), represent the smallest size in individual eggs, averaging 4 mm. in length and 1 mm. in diameter and the eggs of *Brachystola magna* (Girard) the largest, averaging 6 mm. in length and 2 mm. in diameter.

The egg laying methods of grasshoppers are fully described in the literature and will not be further taken up at this time. Criddle (1933a) gives interesting details. The behavior activity of particular significance for this study was the testing of the soils by the females in selecting the particular

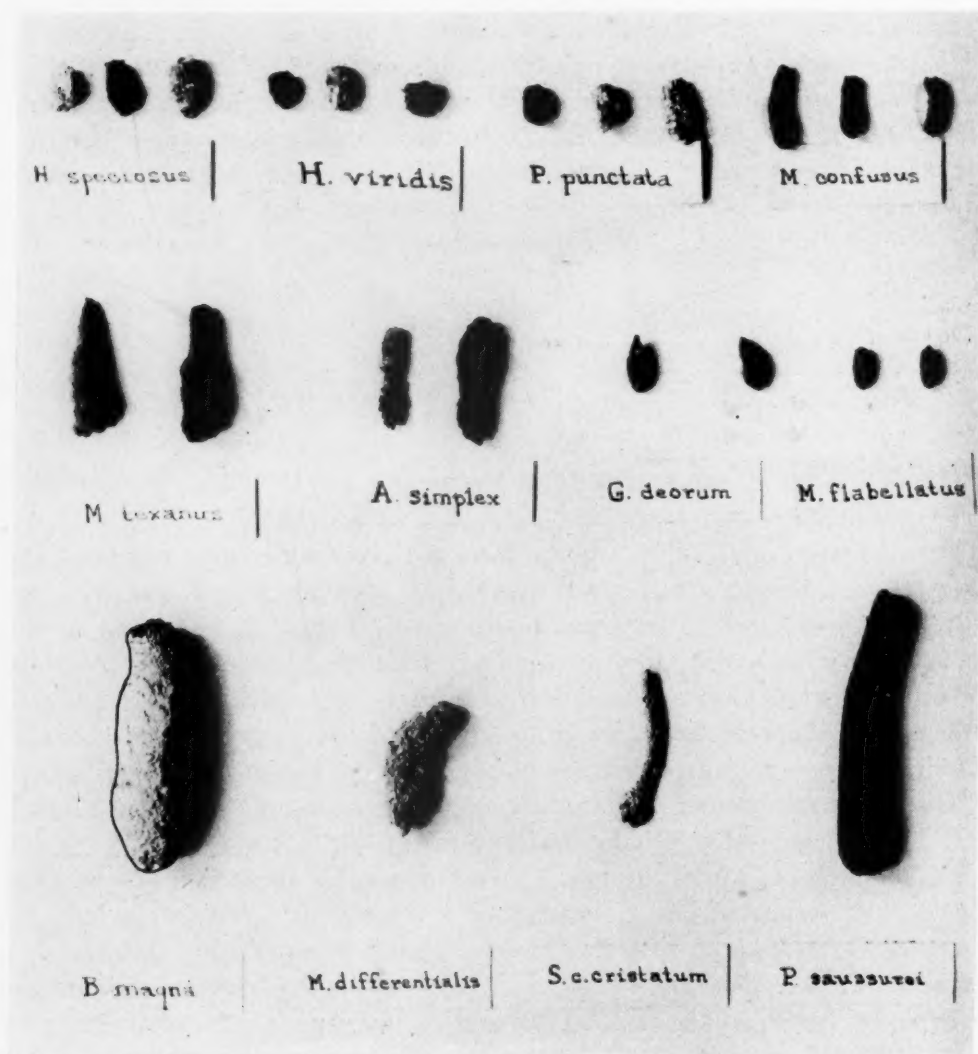


FIG. 7. Typical egg pods of 12 acridian species. For actual sizes (length and diameters) of pods see measurements given in Table 9. Pods with long stoppers are well represented by those of *S. c. cristatum* and *A. simplex*. Pods with relatively short stoppers are shown by *B. magna* and *M. texanus*. Stoppers were essentially absent in pods of *H. v. viridis*.

site for the oviposition of individual packets. In most instances it was observed that a number of tests are made by each individual female before the egg site was finally selected. Knutson (1937) suggests that the female tests the soil with her palps. The most evident testing, however, is done with the ovipositors. Frequently a female will burrow well into the ground and give up the particular site and test again and again before making a final selection. Since these preliminary egg cavities or drill holes are not closed by the female as are the cavities actually used for the egg pods, the soil in our soil pans was often pitted with drill holes. A comparison of the number of drill holes and the number of egg pods actually deposited by certain species is shown in Table 8.

TABLE 8. DRILL HOLES AND EGG PODS

Comparison of the numbers of drill holes and egg pods of *Syrbula admirabilis* Uhler and *Melanoplus keeleri keeleri* (Thos.).

COLUMN HEADINGS:

Dates —Duration of tests.
AvF —Average number females in cage.
Totals —Total egg pods or drill holes.

SOILS:

CrCh —Coarse Chalk or M.a.l.
CrLm —Creek Loam.
CrSd —Coarse Sand.
BICl —Black Clay.
FiSd —Fine Sand.
FiCh —Sifted Fine Chalk.

Acridian Species	Date 1935	AvF	CrCh	CrLm	CrSd	BICl	FiSd	FiCh	Totals
<i>S. admirabilis</i>	6							
Drill Holes.....	0	6	4	6	5	0	21
Egg Packets.....	IX,23-XI,27	0	4	0	0	3	0	7
<i>M. k. keeleri</i>	10							
Drill Holes.....	0	0	4	25	20	3	52
Egg Packets.....	IX,23-XI,27	0	2	0	5	15	2	24

It will be noticed that *S. admirabilis* made 21 drill holes in four different soils (Table 8), but selected only two soils for the laying of seven egg pods. *M. k. keeleri* made 52 drill holes in selecting egg laying sites for the 24 pods which were later deposited. Fifteen of these pods were deposited in fine sand (Table 8).

The average number of eggs per packet of the species represented in Table 9 ranged from 4 to 30. *G. decorum* averaged four eggs per packet, and *B. magna* averaged 30. *X. c. pantherinus*, not shown in the table, averaged 87 eggs for the two packets dissected. This was the largest number for the 32 species studied. Economic entomologists give records of over 100 eggs per packet for *M. differentialis*.

Species associated with sandy soil egg laying sites in nature (*P. saussurei* and *S. c. cristatum*) show a much longer length for the stopper than those acridians which lay their eggs in clay soils. Turf layers (*H. v. viridis*) have the stopper reduced to the minimum.

EGG LAYING SITES—JUVENILES

Undoubtedly the breeding place is of primary significance in determining the habitat of an acridian species. Migratory grasshoppers, chiefly pest

TABLE 9. STRUCTURE OF EGG PODS AND EGGS

ABBREVIATIONS:

Pods. Exm.	—Number of Pods Examined.
Av. Lg. of Pods.	—Average Length of Pods.
Av. Lg. & Dm. Pkt.	—Average Length and Diameter of Packets.
Av. Lg. & Dm. Stp.	—Average Length and Diameter of Stopper.
No. Pods Dis.	—Number Pods Dissected.
Av. Eggs in Pkt.	—Average Number of Eggs in Packets.
Lg. & Dm. of Eggs	—Length and Diameter of Eggs.
--	—Not determined.

All measurements of length and diameter are given in *millimeters*. Where two measurements are given in the same column the top one is for the length and the bottom one for the diameter.

Acridian Species	Pods. Exm.	Av. Lg. of Pods	Av. Lg. & Dm. Pkt.	Av. Lg. & Dm. Stp.	No. Pods Dis.	Av. Eggs in Pkt.	Lg. & Dm. of Eggs
<i>A. simplex</i>	11	30	16 5	14 --	6	25	5 1.5
<i>P. punctata</i>	17	12	9 6	3 5	6	9	4 1
<i>M. texanus</i>	22	27	12 9	15	7	20	5 1.33
<i>P. saussurei</i>	3	54	15 --	39	1	28	5 1.75
<i>S. c. cristatum</i>	8	34	8 5	26 3	5	17	5 1.3
<i>H. v. viridis</i>	8	8	7 7	1.5 4	5	12	4.5 1.3
<i>H. speciosus</i>	25	10	8.5 6	1.5 5	6	15	5 1.5
<i>G. deorum</i>	6	10	8 5	2 2	3	4	5 1.5
<i>B. magna</i>	4	58	50 16	8 9	3	30	6 2
<i>D. pictum</i>	15	15	8 6	7 4	7	8	5 1.5

species, may move far away from the hatching site even in their nymphal stages.¹⁹ After years of persistent field checking I am convinced that, as a rule, among our native species in north central Texas the entire series of juvenile instars is passed in close proximity to the place of hatching. The

¹⁹ Criddle (1926, p. 505) uses the term larval for the first three instar stages and pupal for the fourth and fifth instars. Hebard usually employs the term juveniles for immature grasshoppers.

length of the juvenile period for most species which are hatched in the spring and summer is about five weeks, varying from 30 to 40 days. Life history cycles have been investigated by Carothers, 1923, p. 14; Criddle, 1933a, p. 475; and Shotwell, 1930, p. 20. In north central Texas we have ten species (Isely 1937) which are hatched in the late summer (September) and do not become adults until the last of the following March, or in April, or in May. In several of these species the winter is passed in the first instar, and the entire juvenile period occupies a span of seven to eight months.

HATCHING AREAS AS EVIDENCE OF SOIL CHOICES FOR OVIPOSITION

The grasshoppers that pass the winter as juveniles, as well as a number of other species are very distinctive even in their first instar stages. Such species may be studied as to their local distribution from the time of hatching to maturity through field observations. As already indicated the hatching centers of non-migratory species are essentially the same as the optimum habitats of the species concerned. There are several species, however, where the strong flying adults range rather widely from their egg laying sites. With these latter species the field study of early juveniles will help determine their egg laying soil relations.

Egg-pod surveys are employed by economic entomologists in locating the breeding centers of pest species. However, the so called "non-economic" species with which this paper is chiefly concerned, as a rule, do not occur in sufficient numbers to make the locating of egg pods practical in field surveys. The areas where juveniles are hatching or early instars are found can be used, however, to advantage in locating egg laying sites of these "non-economic" species. My most complete field data concern eight species: (1) Light sandy soil acridians, three species *Pardalophora saussurei* (Sc.) *Spharagemon collare cristatum* (Sc.), and *Melanoplus impiger* Sc. have been studied for several seasons in their early instar stages. These three species have been very abundant in favorable habitats, *M. impiger* even reaching numbers that might be designated as swarming (Isely 1935, p. 324). (2) Eroded sub-soil slope acridians, two species *Trimcrotropis pistrinaria* Sauss., and *Acrolophitus variegatus* (Thos.) have been persistently studied. At their adult peak these species are common, but they do not become abundant even in their optimum habitats. However, these grasshoppers have been found in good numbers and have been continuously checked in field studies for the last three seasons (1935-37). As far as their *soil relations* are concerned, field evidence suggests that the chief index of the habitat of these two species in the blackland prairies of north central Texas is the eroded calcareous sub-soil slopes which mark their chosen optimum habitats. Their juveniles appear only where top soils have been washed away.

(3) Two other species similar in distribution to *A. variegatus* and *T. pistrinaria* are *Xanthippus corallipes pantherinus* (Sc.) and *Hadrotettix trifasciatus* (Say). Their hatching centers are on the tops of hills and ridges,

rather than on the sub-soil slopes. As a consequence the larger area available for suitable egg laying sites results in a wider distribution of the juveniles of these species. (4) Timber margin acridians, *Arphia simplex* Sc. in its adult activity has wide local distribution. Field records show early instar juveniles closely associated with timber margins. Since this species frequents blackland prairie, as well as sandy cross timber habitats, and is a general grass feeder, it seems obvious from its juvenile distribution that shelter is the controlling factor in its choice of egg laying sites rather than soil or specific food plants.

Egg laying sites of several other species have been checked, but not as thoroughly as for the eight species discussed above. These field data emphasize the importance of soil texture, structure, and composition as contributing factors in explaining local distribution of acridians.

GENERAL CONSIDERATIONS

ECONOMIC IMPORTANCE

In America the word grasshopper²⁰ has come to be synonymous with crop destruction. Only three of the forty species checked for their food preferences in these studies belong to "economic" species as they are usually listed by entomologists and experts in grasshopper control (Parker 1933, p. 3459). These species are *Melanoplus differentialis* (Thos.), *Melanoplus mexicanus mexicanus* (Sauss.), and *Brachystola magna* (Girard).²¹ The 37 other acridian species discussed in connection with Tables 1-6 are usually classified by economic entomologists as non-economic and non-migratory grasshoppers. These acridians are, however, of biological interest, economically as well as ecologically. The grass feeders may exact their toll from overgrazed ranges and to this extent may damage the carrying capacity of the range for live stock. Weed-eating species, on the other hand, may be of value to agriculture and rightfully classed as beneficial (Gillette 1904, Ball 1936). All acridians certainly play an important part in biotic interrelationships. In cage tests *Melanoplus differentialis* (Thos.) and *Melanoplus mexicanus mexicanus* (Sauss.) proved to be general feeders. Tests of *Brachystola magna* (Girard) show that this species is rather limited in its food choices. Only certain coarse weeds and cotton have been acceptable as food.

As far as migratory activities are concerned very little evidence was found of migration in search of food by any of the 37 non-migratory species studied. This non-migratory behavior is significant from the economic viewpoint. Field studies (1931-37) show that after the host-plants of certain acridian species wither and die in unfavorable plant habitats, the grasshoppers in these habitats also die and do not migrate to cultivated fields or other pastures where food conditions are favorable.

²⁰ For migratory, gregarious, and destructive acridians Uvarov (1928, p. vii) urges that the term locust should be used.

²¹ In north central Texas *Melanoplus bivittatus* Say, is occasionally found and one would expect to find *Melanoplus femur-rubrum* (DeGeer). However, during the past seven years of field work (1931-37) only one specimen of *M. femur-rubrum* has been collected.

There is always a possibility however that species which find crop plants palatable (Tables 1-3) may to some extent, at least, be a threat as potential pest grasshoppers.

PHYSIOLOGY AND TAXONOMY

The menu differences of *Hesperotettix viridis viridis* (Thos.) and *Hesperotettix viridis pratensis* (Sc.) have been noted by Carothers (1923, p. 10). Field observations and cage studies of the writer show that these sub-species are definitely different in their distribution and in their food preferences. In north central Texas *H. v. viridis* is common and widely distributed. Its preferred food plant, *Amphyachyris*, is an abundant late summer and fall pasture weed. *H. v. pratensis*, however, is found in only a few localities. Its distribution is definitely restricted by the distribution of its favorite host-plant *Solidago petiolaris* Ait. These food selection differences appear to be correlated with the taxonomic differences of these grasshoppers. The question naturally arises are these physiological differences sufficient grounds to warrant the separation of *H. v. pratensis* from *H. v. viridis* and give the former specific rank.

The possibility of hybrids among acridians is always of interest to taxonomists, as well as geneticists and cytologists. I have observed, as have others, a few instances of copulation in cages between *H. v. viridis* and *H. v. pratensis*. Similar pairing behavior was noted occasionally between other species. One unexpected instance was copulation between such widely separated species as *Hypochlora alba* (Dodge) and *Melanoplus plebejus* (Stål).

EXPOSURE OR SHELTER

Shelter afforded by vegetation undoubtedly plays an important role in acridian distribution. Certain species *Trimerotropis pistrinaria* Sauss., *Platylactista aztecus* (Sauss.), *Rehnita capito* (Stål) always live in open habitats on bare soils with only scattered clumps of vegetation, or even on eroded slopes with scant marginal vegetation; others, *Mesochloa abortiva* Bruner, *Opeia obscura* (Thos.), and *Trachyrahachis kioawa fuscifrons* (Stål) frequent low sparse vegetation, buffalo grass, Bermuda grass, clipped golf fairways; still others reach optimum numbers only among tall grasses and weeds, *Syrbula admirabilis* Uhler, *Hesperotettix viridis viridis* (Thos.), *Hesperotettix speciosus* (Sc.); a few frequent the open woods or timber margins, *Spharagemon bolli* Sc., *Chortophaga viridifasciata* (DeGeer), and *Psoloessa texana texana* (Sc.). The above are just a few examples of habitats showing variations in vegetation and cover, which are frequented by different kinds of grasshoppers.

It is obvious that the acridians living in open situations are exposed to all extremes and variations of weather; temperature, humidity, wind, and rain; or desiccation, freezing, sweltering, and drenching. Preliminary experiments suggest that species living in exposed situations will endure

higher ranges of temperature and aridity than the species from sheltered habitats or lush vegetation habitats. Hamilton (1936) points out that his experimental studies suggest that temperature and humidity optima differ not only for different species but for different stages in the life cycle of the same species.

GENERAL DISCUSSION AND CONCLUSIONS

The results of the writer's food-preference experiments and starvation tests clearly establish the fact that specific plants are required as food by many acridian species of north central Texas. Food tests in which an abundance and variety of fresh plant food selected from the host-plant menu of certain acridian species, when offered to other grasshopper species, proved in many instances to be wholly unpalatable even to the point of starvation. These experiments show that vigorous individuals of many species will starve in the presence of an abundance of vegetation if their host-plant species are not included in the foods offered.

It is evident from these data if specific grass feeders are included that over 75 per cent of the 40 species studied in the writer's cages were selective in their diet choices and were definitely oligophagous. Oviposition behavior further emphasizes the need of specific diet for individual maintenance and normal egg laying.

The experimental findings of these studies are in the main at variance with other investigators who have studied the relations of the Acrididae to plants or have reviewed literature on this subject. Uvarov (1928, p. 92) "Vegetation does not, however, influence the selection of habitat by many Acrididae as food because of its food value." Ross (1934, p. 128) "In many other groups of phytophagous insects the distribution of insect species is dependent primarily on distribution of the food plant. This is not true of the Orthoptera probably with few exceptions, such as *Inscudderia taxodii*, which is always found upon cyprus foliage." Vestal (1913, p. 77) "There is very seldom any direct relation between grasshopper species and species composition of the plant associations, as few grasshoppers are selective feeders." Golding (1934, p. 278) "The choice of habitat is not usually dependent on the vegetation *per se*."

The writer's experiments, on the other hand, point to the fact that many species of the Acrididae depend upon a limited number of plants for species maintenance. It is obvious, therefore, that plant species as food play an important role in distribution of many species of grasshoppers. However, other environmental factors are important in the make-up of a habitat complex when all different acridian species are considered. Among these other factors²² soil texture, soil structure, topography, exposure, and vegetation as cover have been discussed. All of these must be evaluated in determin-

²² Facilities were not at hand to determine soil moisture and pH. Soil moisture is, on the one hand related to soil texture, and on the other hand correlates with vegetation as cover for shade.

ing local distribution. Mere abundant growth of vegetation of the right plants for food is by no means the only criterion for acridian optimum living conditions. For example, a hillside slope covered with a pure stand of *Evax* has been examined and not a single specimen of *Acrolophitus variegatus* (Thos.) found although its host-plant (*Evax*) was everywhere abundant and *A. variegatus* was frequent in neighboring pastures where other conditions for its living were supplied. Eroded ridges with occasional plants of *Hymenopappus* are favored by *Trimerotropis pistrinaria* Sauss., rather than more level tracts with a solid cover of its favorite food plant, *Hymenopappus*. Other instances may be multiplied. The point at issue, however, is that specific plants, or at most a limited number of species, are among the *minimum conditions* necessary for species maintenance for many of the Acrididae. Specific plants as food cannot be left out of the picture and must be taken into account in explaining *local distribution of acridians*.

SOILS VS. VEGETATION

The writer's field evidence concerning soils chosen for oviposition by female grasshoppers of several species is more definite than are the results of his experimental studies obtained by testing the reaction of female acridians to different types of soil in cages. Table 7 gives suggestive data concerning the egg laying behavior of eighteen species. A few species, however, either did not react favorably to cage environments, were not supplied with the right kinds of foods, or their eggs were not matured. At least, very few egg pods were obtained although adult females were kept in cages for several weeks.

The types of soils, plants for food, vegetation for shelter and protection are among the environmental factors which suggest the grouping of the acridians studied into four classes: (1) The distribution of certain species seems clearly correlated with specific soil types. In certain cases (a) soil texture, such as sandy, sandy loam, clay loam, or clay (Weaver and Clements 1929, p. 168), appears to determine the soil choices, and in other cases (b) soil structure becomes the determining factor in the form of compact roadways, field margins or eroded hillsides. (2) Other species are limited in their local distribution by the presence of specific plant species for food. (3) Still other species depend on vegetation for shelter and protection. (4) There is a broadly tolerant class whose species appear to adjust themselves to variations in soil and vegetation.

In the main these affinities appear to follow taxonomic sub-family cleavages. (1) The Cyrtacanthacrinae are more definitely associated with specific plants for food. (2) The Acridinae are often dependent on plants for shelter and protection. The elongated body form of certain species simulates the shape of the upright culms of the tall prairie grasses; other Acridinae belonging chiefly to species of smaller size are somewhat flattened in body form, these are associated with low matted grasses. (3) The Oedipodinae are

the premier soil grasshoppers and are more obviously soil-related, not only in color and form, but even in oviposition behavior. Species of this sub-family, on the one hand, are clearly related to vegetation for shelter, shade and the resulting higher humidity [*Arphia simplex* Scud., *Chortophaga viridifasciata* (DeGeer)] or on the other hand there are species which are adapted to endure extremes of aridity and exposure where the vegetation is sparse [*Trimerotropis pistrinaria* Sauss., *Rehnita capito* (Stål)]. These variations in conditions have to be evaluated in explaining the distribution and soil relations of the Oedipodinae. (4) The Cyrtacanthacrinae and the Oedipodinae both contribute to a broadly tolerant or highly adaptive group. Certain species of these two sub-families are mixed feeders. These species frequent soils of varying texture although there is doubtless much uniformity in the matter of soil structure, as well as similarity in their shelter relations.

There are a number of clean-cut exceptions to the sub-family grouping I have suggested above. *Acrolophitus variegatus* (Thos.) is an interesting exception. In fact the collector who has studied the taxonomy of acridian sub-families would place this species with the Oedipodinae when first taken instead of the sub-family Acrididae. Even in its behavior *A. variegatus* lines up with the Oedipodinae. It frequents bare soils or rests on low, flat, broad-leaved plants. Another exception is found in *Psoloessa t. texana* (Sc.). This species and *A. variegatus* are more definitely soil related than any other species of the Acridinae of north central Texas. Several other exceptions might be given. In general, however, the affinities as outlined above will bear close field scrutiny.

SUMMARY

1. Many acridian species are selective feeders and are essentially oligophagous.
2. A few of the oligophagous grasshoppers approach monophagy.
3. Of the two chief north central Texas (1931-1937) economic species *Melanoplus differentialis* (Thos.) is strikingly polyphagous but *Brachystola magna* (Girard) is oligophagous.
4. Less than 25% of the species experimentally tested in cages were mixed feeders and, appeared to even approach polyphagy.
5. The Acridinae and Oedipodinae were primarily grass eaters, selecting widely among the grasses offered in cages; however, under primitive conditions of the blackland prairies the number of species of grasses available was undoubtedly limited.
6. The Cyrtacanthacrinae fed chiefly on forbs. Selective feeders are more generally found in this sub-family than among the Acridinae, Oedipodinae, or Batrachotetrigininae.
7. Starvation food experiments prove that selective feeders will starve in cages if deprived of their host-plants even in the presence of abundant fresh host-plant materials palatable to other species of the Acrididae.

8. A thorough understanding of acridian taxonomy with a knowledge of plant species is necessary before even a beginning can be made toward a comprehensive diagnostic analysis of local distribution of the Acrididae.

9. Soil factors which control the local distribution of plants are secondarily controlling factors of acridian distribution.

10. A few acridian species, especially among the grass eaters, appear to have identical menus, and in the field they show similar reactions to environmental conditions of exposure or shelter as the case may be. Their soil relations, however, are definitely different. For these species soil relations may be primary in determining their local distribution.

Soil structure appears to be more important in delimiting egg laying sites than soil texture; however, soil texture gives invaluable field clues in the marking off of terrestrial habitats.

11. The adaptation of certain acridians to introduced species of plants (Bermuda grass, Johnson grass, crop plants, et al.) has complicated the problem of local distribution.

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THE OYSTER "LEECH," *STYLOCHUS INIMICUS*
PALOMBI, ASSOCIATED WITH OYSTERS
ON THE COASTS OF FLORIDA

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THE OYSTER "LEECH," *STYLOCHUS INIMICUS* PALOMBI, ASSOCIATED WITH OYSTERS ON THE COASTS OF FLORIDA

INTRODUCTION

Among the pests which have decreased the productiveness of oyster beds on the Atlantic and Gulf coasts of the United States the polyclad worm which is known to Florida fishermen as the oyster "leech" has often attracted unfavorable attention. This flatworm has been reported to occur from Pensacola Bay on the west to Indian River on the east. At Tampa it has been known for more than thirty years, and according to Danglade (1919) it has become abundant enough to do considerable damage every few years. In 1906-1907 it destroyed oysters along the Indian River. In 1916-1917 it did much damage to beds at Cedar Key, Port Inglis, and Tampa. More recently the oyster leech has been abundant in Apalachicola Bay. Dr. H. F. Prytherch of the Beaufort Laboratory of the Bureau of Fisheries was sent to investigate conditions. In a typewritten report concerning his findings he says:

A few specimens of the wafer "leech" have been found by oystermen in Apalachicola Bay at various times in the past but not until 1932 had it become sufficiently abundant to seriously affect oyster production on natural bars. In November of that year the Bureau's investigation showed from 50 to 75 percent of the large oysters on Porter's Bar had been killed by the wafer and that approximately 25 percent of the live oysters contained one to four parasites each. During the following year all the oysters on this area were killed as well as a high percentage of those on adjacent natural beds known as Platform Bar, Green Point Bar, and North Lump. A recent survey of the above areas in October 1934 showed not only complete destruction of adult oysters but also a high and parasitic infection of the seed oysters which had attached here within the last year. It was evident that the parasite was spreading rapidly to other areas to the westward as it was found at several points on St. Vincent Bar, a distance of 12 miles from the original outbreak and on Bulkhead Bar, both of which are the largest natural oyster beds in this region.

The oyster industry in Apalachicola Bay began in 1836. Swift (1897) made a careful survey of the bay in 1895-1896 and published an excellent map. He states that,

The destruction of the beds in St. Vincent Sound and Apalachicola Bay was due somewhat to their being overworked, but principally to the following causes: The freshet of 1893, the hurricane of October 8, 1894, a very severe freeze in the latter part of December of the same year, and another very heavy hurricane on February 13 and 14, 1895. There had been previously (in January, 1886) a heavy freeze that killed many oysters; so that few were taken the following season, and in 1888 a freshet seriously affected the beds.

It seems to be the general opinion that the beds are deteriorating at Platform, Bulkhead, and Cat Point bars, where oystering is going on at present, and the reason assigned is that beds are overworked, the demand being too great for the supply. As far as known there seem to be no enemies of the oysters on the beds, unless the boring clam . . . and the algae found on the oysters of the East Hole Bar may be called enemies.

Again in 1915 Danglade (1917) surveyed and mapped Apalachicola Bay. He says "the oysters of these waters have no aggressive enemies, and no diseases were observed. Physical phenomena, however, have greatly damaged many of the bars." Soon after this, early in 1917, oyster leeches were reported as doing damage to beds at several points on the east coast of Florida and Danglade (1919) made an investigation. He found that leeches were most abundant on bars where salinity was high. "When the devastation was at its height the affected oysters, as a rule, contained from 1 to 3 worms, although as many as 8 or 10 are said to have been taken from a single oyster . . . in Tampa Bay . . . mature and young oysters alike were said to have been completely annihilated. . . . At Port Inglis and Cedar Key . . . no small oysters were found or reported containing worms."

The writers of the present paper were asked to go to Florida to study the oyster leech for the Bureau; and spent eleven months beginning June 1, 1935 in Apalachicola Bay, with short trips to other parts of the state. Two species of oysters, *Ostrea virginica* Gmelin and *O. equestris* Say, were found on the bars in Apalachicola Bay. With these, two species of polyclad worms were regularly associated and eight other species of polyclads were present at times. The work was carried on at the Indian Pass Laboratory of the Bureau. It is a pleasure to make the following acknowledgments: Mr. Elmer Higgins offered the opportunity to carry on the work and did everything possible to make it a success; Dr. Paul S. Galtsoff gave encouragement and valuable advice; Dr. H. F. Prytherch turned over all records of his work on polyclads in Florida and made many helpful suggestions; Mr. George S. Hiles, Jr. determined routine salinities for the laboratory until March 1; Captain Frederick Sawyer and Herbert D. Lane, crew of the boat *Virginia*, gave most excellent, cheerful, and competent service in collecting and helping in the examination of materials from the oyster bars; and Mr. R. O. Smith helped in administrative matters. A number of specialists identified certain of the animals collected and grateful acknowledgment is made for their services: algae, Dr. H. L. Blomquist; coelenterates, Dr. Oskar Carlgren; polychaetes, Dr. A. H. Treadwell; echinoderms, Dr. C. B. Wilson; amphipods, Mr. C. R. Shoemaker; isopods, Mr. J. O. Maloney; anomurans and macrurans, Dr. Waldo Schmitt; crabs, Dr. Mary J. Rathbun; bugs, Dr. H. B. Hungerford; insect larvae, Dr. J. G. Needham; molluscs, Dr. Paul Bartsch and Harold Rehder; ascidians, Dr. W. G. Van Name; fishes, Dr. S. F. Hildebrand.

ANATOMY

Stylochus inimicus Palombi 1931 is classified as follows: Platyhelmintha, Class Turbellarea, Order Polycladida, Suborder Acotyline, Section Craspedommatina, Family Stylochidae, Subfamily Stylochinae; hence is characterized by a flat, leaf-like, firm, parenchymatous body; ciliated integument; ventral mouth, plicated pharynx, and many-branched enteron; brain surrounded by a parenchymatous capsule; reticulate nervous system with several chief longitudinal trunks; nuchal tentacles, but none on margin; marginal, tentacular, cerebral, and frontal eyes; no statocysts; hermaphroditic genital system; male genital apparatus anterior to female and both near the posterior end; reproduction only by sexual means; development results in a ciliated pelagic larva; adult is free-living or commensal.

GENERAL FORM AND SIZE—The body is flat, elliptical and often has the margins wrinkled slightly. The largest specimen from Apalachicola Bay when alive and extended measured 51 mm. long and 27 mm. wide while crawling actively; resting, 40 by 31 mm. It was collected on Porter's Bar, November 7, 1935. The whole surface of the body is covered with close-set cilia, which range from 0.001 to 0.005 mm. in length.

COLOR—The dorsal side is generally gray, with lighter margins and a light band along the middle of the median line. The ventral surface is gray to dirty-white at the margins and grows lighter toward the center, where there is a large white spot caused by the pharynx and parts of the reproductive organs showing through the integument.

ENTERON—The mouth is a small opening (Fig. 1, m) nearly in the center of the ventral surface. It opens into a pouch which contains the pharynx and this leads into the median stem of the gastro-vascular system. The elongated pharynx has about six pairs of folds along its sides. These may be extended through the mouth when food is being swallowed (Figs. 2, 3, 4). From the median enteric stem branched caeca extend almost to the margins of the body: 1 anterior, 1 posterior, and about 8 pairs lateral.

NERVOUS SYSTEM AND SENSE ORGANS—At about the posterior margin of the anterior fifth of the body are two slightly tapering, conical dorsal tentacles. In a moving individual these are about 0.5 mm. long and 2.0 mm. apart. They are usually symmetrically disposed on either side of the body but in some individuals one tentacle may be more or less anterior to the other. The tentacles are retractile and may be withdrawn completely into non-pigmented depressions in the dorsal surface. Between the tentacles is a ganglionic mass. From this four nerves extend forward, three laterally, and a slender dorsal and a heavy ventral pair posteriorly. There are many connections between the principal nerves so that the whole system forms a nerve net (Fig. 5). Along the margins there are also many fine connections between the smaller nerve twigs, and thus a delicate reticulum is built up. A typical adult leech possesses perhaps 1,600 black eye spots. Those in the

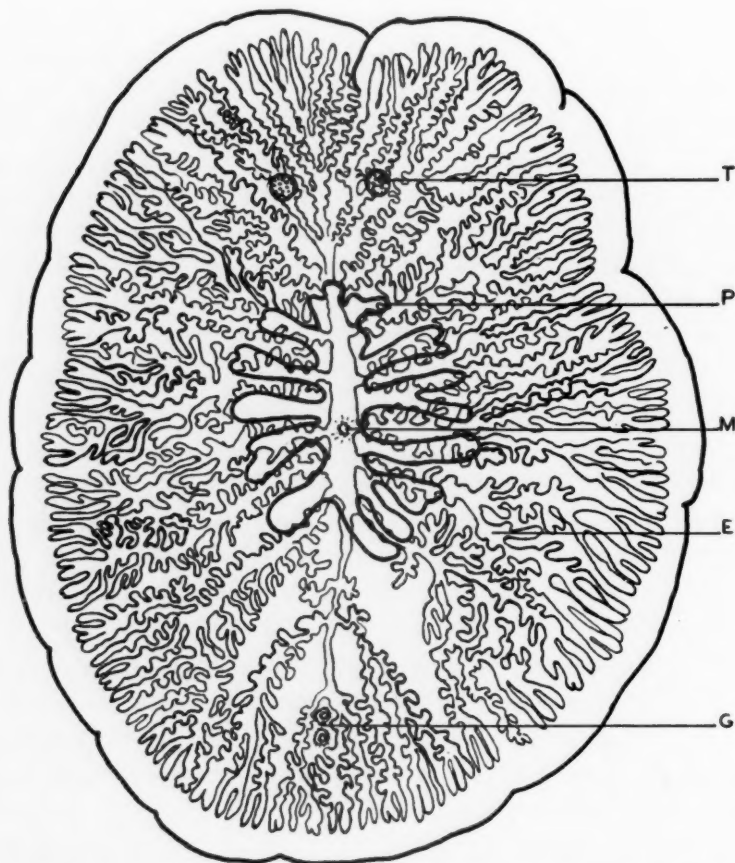
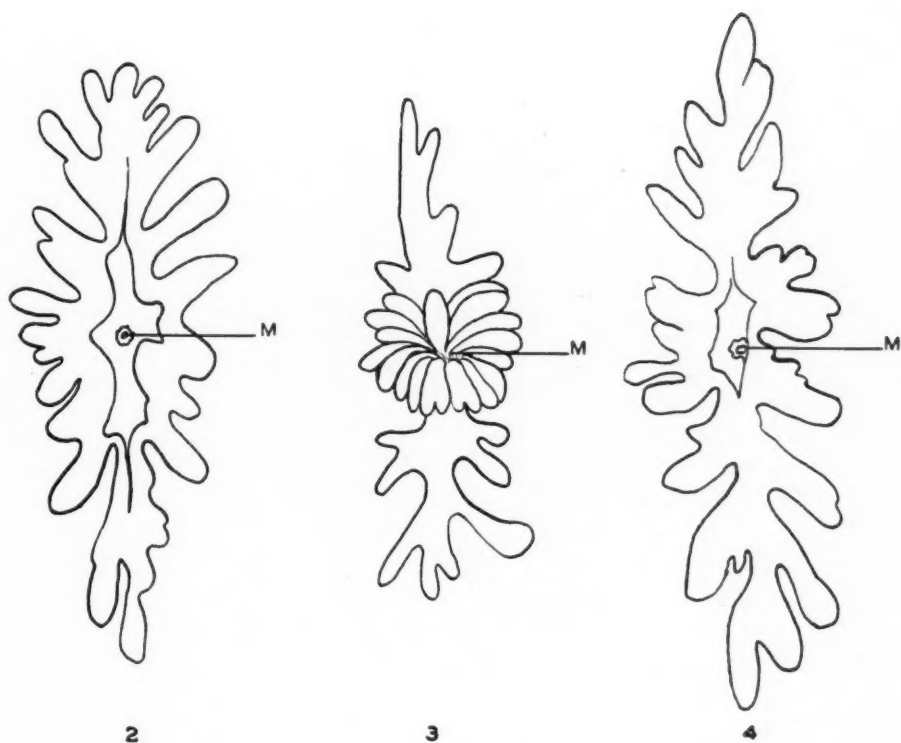


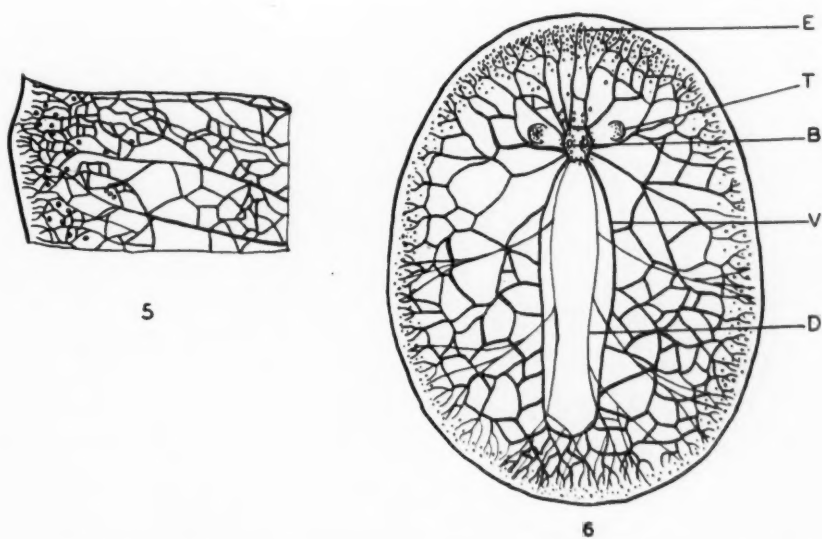
FIG. 1. Enteron of *Stylochus inimicus*. E, lateral branch of enteron; G, genital openings; M, mouth; P, pharynx; T, nuchal tentacles.

tentacles are largest; those at the anterior margin are rather large and there is a general decrease in size and number toward the posterior end, but there are fewest along the postero-lateral margins. The eye spots in an adult leech are distributed as follows: proximal four-fifths of tentacles, 80; two irregular rows of spots dorsal and anterior to the cerebral ganglia, 160; anterior quarter of margin, 720; anterior half of margin, 920; posterior half of margin, 440; posterior quarter of margin, 220.

GENITALIA (Fig. 7)—The male genital opening is in the median line one-seventh of the length of the body from the posterior end. It is surrounded by an oval muscular area. This is doubtless concerned with the protrusion of the penis which lies immediately inside of and anterior to the opening. The duct from the fuzzy prostate gland and that from the seminal vesicle join anterior to the penis to form the short ejaculatory duct. The prostate gland is just dorsal and anterior to the penis. The seminal vesicle is ventral and slightly anterior to the prostate gland. From the seminal vesicle two twisted vasa deferentia lead antero-laterally and may be traced respec-



FIGS. 2-4. Pharynx in various stages; in 3 it is being extended through the mouth, *M*.



FIGS. 5-6. Nervous system. 5, detail to show distribution of nerve twigs and eyes along left anterior margin. 6, plan for whole body; *B*, brain; *D*, dorsal nerve trunk; *E*, marginal eyes; *T*, nuchal tentacle; *V*, ventral nerve trunk.

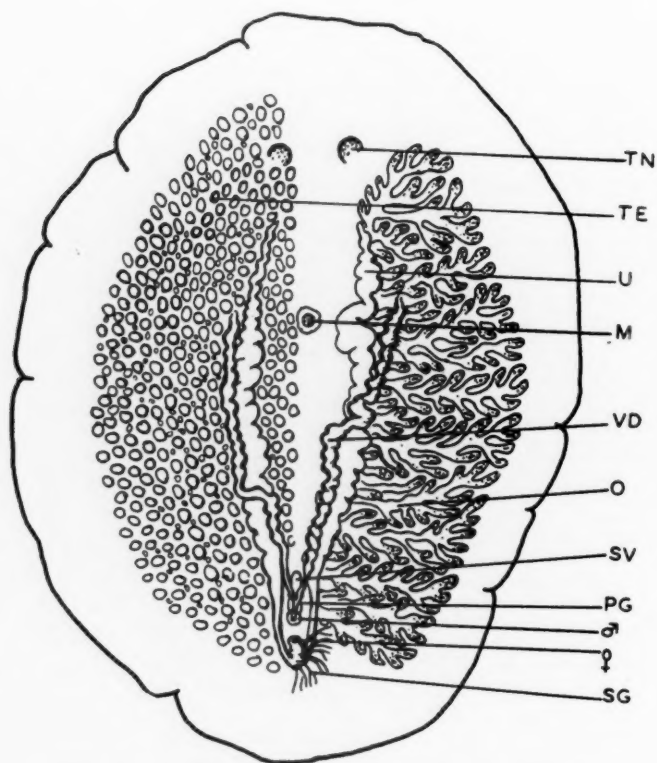
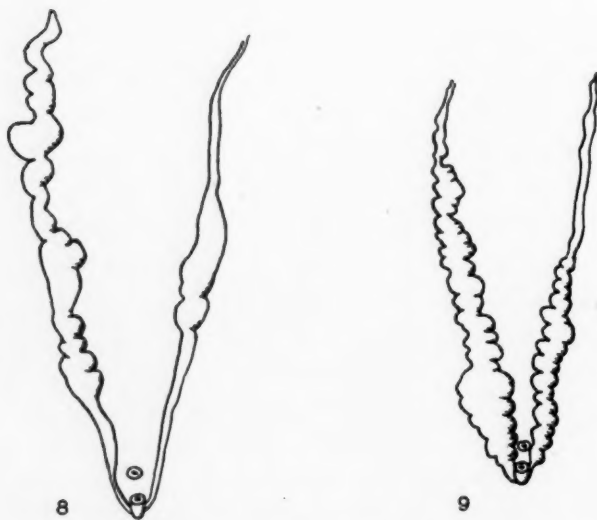


FIG. 7. Genital system: *M*, mouth; *O*, ovarian follicles; *PG*, prostate gland; *SG*, shell gland; *SV*, seminal vesicle; *TE*, testes; *TN*, tentacles; *U*, uterus; *VD*, vas deferens; ♂ male; ♀ female.



FIGS. 8-9. Two pairs of uteri distended with eggs.

tively to points about halfway between the mouth and the lateral margins. On each side about 350 testes of various sizes are scattered through most of the available space. The longest of the testes measure about 0.02 mm. The female genital opening is about 0.2 mm. behind that of the male. It leads into a short (0.2 mm.) vagina. This in turn is connected with two lateral curved uteri which extend forward latero-dorsal to the vasa deferentia and end lateral to and about 0.3 mm. behind the tentacles. From the uteri oviducts and ovarian tubules extend laterally to within 0.2-0.5 mm. of the margin. The tubules are branched somewhat and end in blunt tips.

SECTIONS—Transverse and sagittal sections of individuals were mounted and stained with hematoxylin and eosin. They show no essential differences from the descriptions and figures published by Palombi (1931, 1936). It therefore seems unnecessary to discuss them.

LIFE HISTORY

BREEDING—The eggs of *Stylochus* are fertilized internally by spiral spermatozoa (Fig. 11) about 0.04 mm. in length. Fertilized ova are stored in the paired uteri. In the field eggs were found adhering to the clean inner surfaces of old shells on the oyster bars from the beginning of our observations (June 1) until January 11, but the last eggs failed to develop when brought into the laboratory and may have been laid sometime previously and killed by low temperatures. Throughout the summer when several individuals were placed together in a dish in the laboratory they were seen crawling backwards with the posterior end elevated and the penis extended. Copulation was carried on for as long as nine hours. One pair copulated for five hours on one day, separated, and began again the next day. Several individuals copulated more than once; some at least four times.

OVIPOSITION AND FECUNDITY—*Stylochus* readily deposits eggs on hard surfaces and then broods them for days. Inside old shells on oyster bars

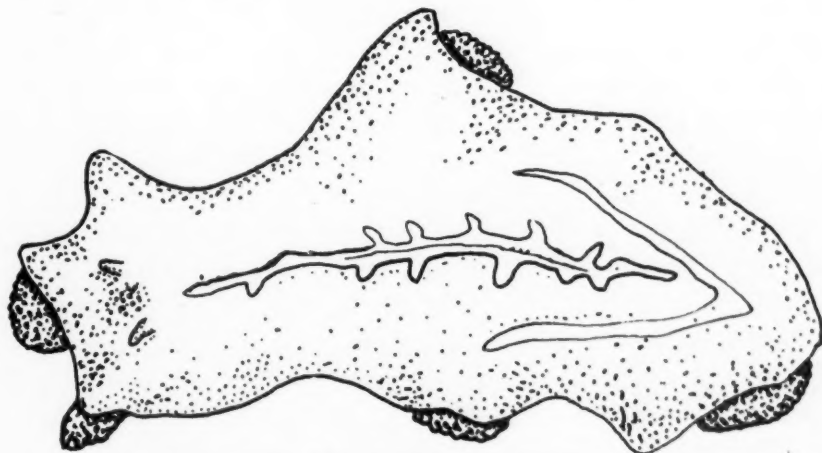


FIG. 10. Shape assumed by a *Stylochus* brooding a large group of eggs that had been laid by several individuals.

and in finger bowls in the laboratory many clutches were observed. Eggs are laid in irregular masses which are a single layer thick. Each egg is enclosed in a shell (Fig. 11), the diameter of which is about 0.18 mm. When fresh-laid the shell is sticky and adheres to the surface below it and to other shells in its group. The brooding instinct is very strong. In September some *Stylochi* were kept together in a dish and several contributed to a large, irregular mass of eggs. One large individual then spread itself into a very bizarre shape (Fig. 10) in order to cover the mass and so remained from September 3 to 11—eight days. In the field single *Stylochi* were often found brooding clutches of eggs which all appeared to have been laid by one individual. Six clutches were carefully counted under a binocular microscope and were found to number: 18028; 17267; 15025; 14252; 11275, and 9158. In the laboratory 35 individuals with full uteri were selected for observation and 31 clutches of eggs were obtained. Six individuals which were kept separately in finger bowls without food laid eggs as follows:

No. 1—July 30, 15072; August 14, 5979; August 21, 919; total, 21970.

No. 2—July 30, 14022; August 15, 1970; total, 15992.

No. 3—July 29, 10179; August 7, 3190; total 13369.

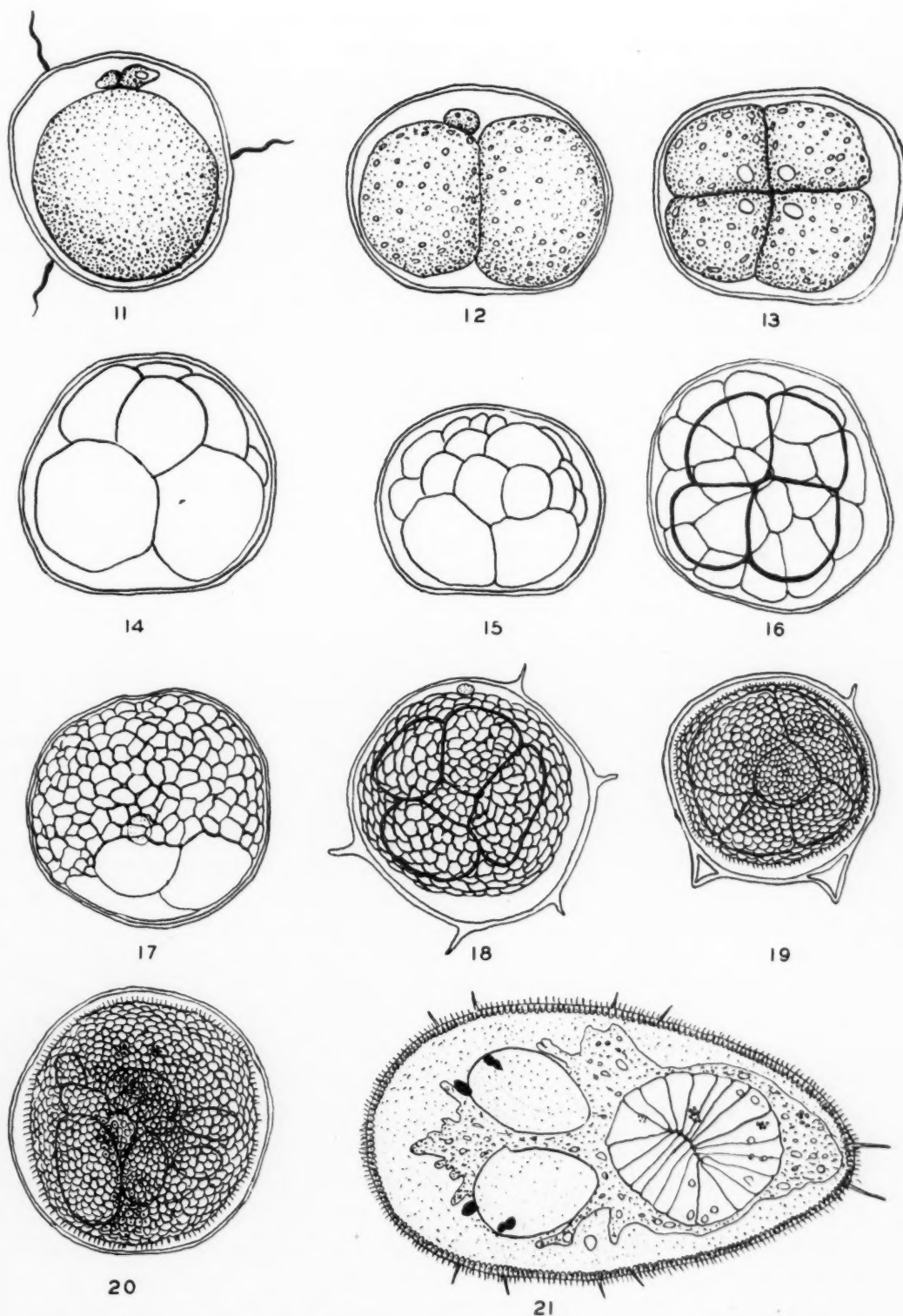
No. 4—July 29, 7351; August 15, 1509; August 21, 2447; total, 11307.

No. 5—July 27, 9075.

No. 6—July 27, 7818.

Of course any or all of these worms may have laid eggs before they were brought into the laboratory. Most of the eggs seemed to be fertile and developing normally. Eggs were not always in the 1-cell stage when laid. For example, six clutches when deposited in the laboratory on July 4, 1935, were in the following cell stages: 1-cell stage, 1 to 2-cell stage, 1 to 8-cell stage, 4 to 16-cell stage, 4 to 16-cell stage, and 8 to 32-cell stage.

EMBRYOLOGY (Figs. 11-21)—Eggs in different clutches appeared to develop at about the same rate (depending on temperature, salinity of medium, etc.), but there were often variations in the time which elapsed between stages. During cleavage the following intervals were observed in times required to pass from one stage to the next at 28.0°C. 1-2 cells, 1 h. 9 m., 2 h. 17 m.; 2-4 cells, 2 h. 41 m.; 4-8 cells, 4 h. 10 m., 34 m.; 8-12 cells, 3 m., 10 m., 3 m.; 12-16 cells, 5 m., 7 m., 3 m., 27 m.; 16-32 cells, 1 h. 45 m., 2 h. 36 m., 2 h. 26 m. At room temperatures (28°C. \pm) in the laboratory eggs required about 11 days to hatch. Progress was about as follows each day: (1) 64 cells, (2) epiboly partly completed, (3) ciliated epidermis and embryo rotating slowly within the egg shell, (4, 5, 6) cilia visible on outside and embryo rotating more rapidly, (7) two eyes present, (8) four eyes present, (9) four eye spots persisted, two posterior setae and a ventral mouth appeared, (10) six eyes present, (11) ciliated, 6-eyed larva hatched.



FIGS. 11-21. Cleavage and development of *Stylochus* larvae. 11, three sperms about an egg with two polar bodies; 12, two cells; 13, four cells; 14, eight cells, micromeres and macromeres; 15, thirty-two cells (lateral); 16, thirty-two cells (ventral); 17, epiboly taking place; 18, epiboly completed; 19, ciliated embryo rotating within egg shell; 20, embryo with two eye spots; 21, larva at time of hatching; B, brain; E, eye spot; G, enteron and unabsorbed yolk cells; P, pharynx.

When eggs were deposited a polar body was usually apparent at the animal pole. It often divided into two or more cells; and sometimes appeared to multiply into a mass of many cells. It often persisted as an appendage to the developing embryo or as a free body within the shell. In 2- and 4-cell stages blastomeres were nearly equal in size, but in the 8-cell stage four micromeres and four macromeres were formed. The micromeres divided more rapidly, and during the second day began to overgrow the larger, yolk-laden macromeres (called micromeres by MacBride 1914). After the macromeres were invested by ectoderm they retained their identity for a day or two but soon broke up into irregular masses which gradually accumulated considerable pigment. Eyes were first present on the seventh day. They apparently increased in number by division of the first pair formed. When first deposited shells were creamy white as seen with the naked eye, but when ready to hatch were covered with a brown coating.

PELAGIC LARVA—After hatching, the ciliated, setose larva (Fig. 21) soon began to swim about. It took an erratic course, continually whirling about, but groups of larvae congregated near the surface of dishes where light was most intense. Many were caught above the surface film and died on the sides of dishes. Larvae swam at the rate of about 1.32 mm. per second at 25°C. One larva swam upward 115 cm. through a glass tube (which had a bore 12 mm. in diameter) in 12 minutes and 30 seconds. Larvae appeared to be strongly positively phototropic, slightly negatively rheotropic, and rather unresponsive to gravity and temperature variations.

GROWTH—On February 7, 1936 ten *Eustylochus meridianalis* were placed in separate finger bowls in sea water that had a salinity of 15.8 0/00. They were given oyster and fresh sea water (15.8 0/00) on alternate days. Two died on February 18 without growth; another on February 24; five others on March 5. The remaining worm ate oyster and increased in length as follows: February 8, 1.5 mm.; February 18, 2.5 mm.; February 24, 3.5 mm.; March 5, 4.5 mm.; March 22, 10 mm.; March 31, 10 mm.; April 2, 12 mm. On the last date it was sexually mature, and apparently in good condition. The same individual was taken to Beaufort, N. C. It was fed oyster until May 16, and had then attained a length of 20 mm. It grew to maturity in less than two months. This *Eustylochus* was fixed, imbedded, sectioned, and stained. Spermatozoa and ova were found to be abundant in its vasa deferentia and uteri. It had never been with another individual, and had therefore not copulated.

On March 5 two lots of five each of *Eustylochus* were fed on alternate days; one with oyster and the other with barnacle. The results of this work are summarized in Table 1. These results show that the growth of *Eustylochus* may be quite rapid under favorable conditions.

Stylochus also grows rapidly. At Oslo and St. Lucie, Florida, seventy-seven *Stylochi* were collected on April 7 and 8, but none were taken when

TABLE 1. GROWTH OF *Eustylochus meridionalis* FED ON OYSTER OR BARNACLE

Date	5 specimens fed oyster				5 specimens fed barnacles			
	Eyes		Length		Eyes		Length	
	Average Number	Per cent Increase	Average mm.	Per cent Increase	Average Number	Per cent Increase	Average mm.	Per cent Increase
March 5	12	0	1.6	0	13.8	0	1.4	0
March 14	20	40	1.9	19	23.8	101	2.6	100
March 22	Dead ¹		Dead ¹		75.0	543	5.2	207

¹These were apparently killed by the fouling of water by spoiled oyster.

buckets of shells collected from oyster bars were allowed to stand overnight. All but five of these specimens were of large size and thirty-four of them were brooding clutches of eggs. The larger individuals had probably passed the winter in a rather mature condition and began to breed early in the spring. The largest individuals measured 25 to 48 mm. in length; the five small individuals, 10-20 mm., ave. 14.6 mm. The latter were fed oyster from April 9 to 20 at the Indian Pass Laboratory and then shipped to Beaufort, N. C. where they were fed oyster daily until May 20. At the beginning of the experiment at Beaufort their average length was 12 mm. and their average weight 0.0366 grams. During three weeks their length increased 43% and their weight 112%, i.e.; to 17.2 mm. and 0.775 grams. Probably most *Stylochi* live less than one year.

STARVATION—Five specimens of *Stylochus inimicus* were kept in separate covered finger bowls in the laboratory from November 18 to March 5, without changing the water in the dishes or feeding the worms. After March 5 two of the worms were placed together in a dish. These individuals were fed oyster every other day and fresh sea water was used in their bowl. The other three worms were kept as before. The two fed worms apparently ate nothing, but became active and copulated. On November 18 the length of the worms was respectively: 30, 25, 23, 23, and 20 mm.; on March 5 it was 12, 22, 20, 18, and 11 mm. All had decreased in size. The third and the fifth in the list laid eggs on or before November 29. One of these starved *Stylochi* lived until May 21 at Beaufort, N. C., a total of 185 days without food.

PHYSIOLOGY

LOCOMOTION—Below 12°C. and above 34°C. *Stylochus* usually curled up and did not attach itself to the substratum. The righting reaction appeared to give a better index of the activity at different temperatures than actual rate of locomotion, as the curve in Figure 22 shows. On a smooth glass or celluloid surface, tested in sea water having a salinity of about 20 0/00 *Stylochus* crawled at the following rates in millimeters per minute:

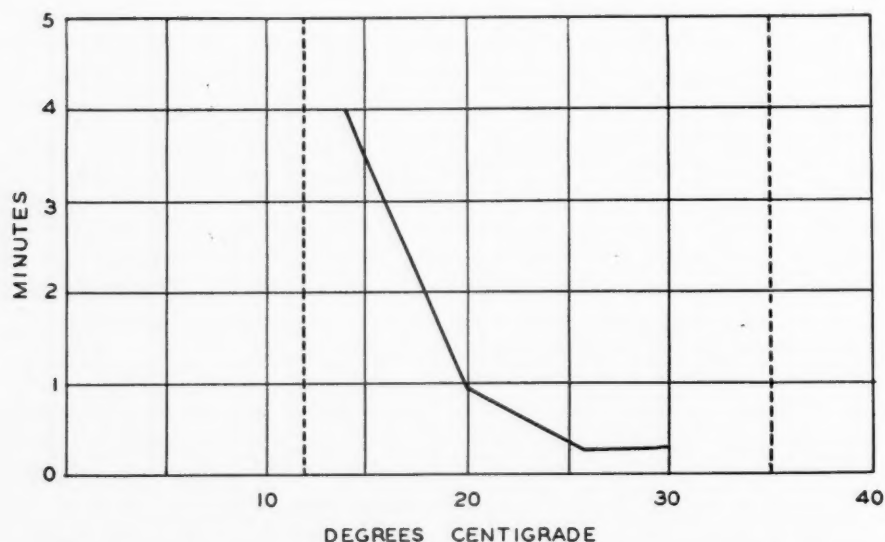


FIG. 22. Average time, in relation to temperature, taken by *Stylochus* which had been turned with its ventrum uppermost to right itself and become attached to the substratum. The vertical dotted lines indicate the thermal limits of attachment.

14°C., 6.6; 14.9°C., 15.6; 19.7°C., 26.4; 23°C., 35.4; and 25°C., 39.2. Of course large individuals usually moved faster than small, and there was considerable individual variation. Stylochus crawls on the edges of its body so that there is a cavity below. It continually jerks its anterior margin, now in one region and again in another, as it moves forward. The tentacles are turned forward a little. Often an individual may crawl backward for a short distance. A Stylochus is readily fatigued. One individual moved 85 cm. at an average speed of 35.4 mm. per minute. At the beginning it moved 52.8 mm. per minute, at the end, 27.6 mm. *Eustylochus meridionalis* is active at lower temperatures and in general moves more rapidly than Stylochus; as the following rates in millimeters per minute show: 7°C., 0.12; 12°C., 19.8; 14°C., 26.4; 15°C., 24.0.

PERMEABILITY—At the suggestion of Dr. Paul M. Gross preliminary experiments on the behavior of eggs in a graded series of salinities were performed in the hope that they might throw some light on the permeability of egg shells. On December 3 eggs of *Stylochus* were collected from Crooked

TABLE 2. EFFECT OF IMMERSING *Stylochus inimicus* "EGGS" FOR THIRTY MINUTES IN HYPO- AND HYPER-TONIC SOLUTIONS OF SEA WATER; AT 13.6 C. a, ALIVE; ar, ALIVE AND ROTATING; d, DEAD

[illegible]

TABLE 3. EFFECTS OF IMMERSING *Stylochus inimicus* EGGS FOR ONE HOUR IN HYPO- AND HYPER-TONIC SOLUTIONS OF NaCl, AFTER BEING KEPT IN SEA WATER OF SALINITY 25 ‰ WHERE EGGS HAD AN AVERAGE DIAMETER OF 0.140 MM.
a. SOME ALIVE; d. DEAD; dd, DEAD AND DISINTEGRATING; f. FLOATING

Salinity gms. per l.	0	5	10	15	20	25	30	35	40	45	50
Diameter mm.188	.207	.163	.152	.153	.142	.139	.146	.155	.160	.162
Condition.	dd	d	d	a	d	d	d	df	df	df	ddf

Island Sound where salinity was 33.4 ‰. These were in about the fourth day of development (Fig. 19), with ciliated eyeless embryos within the egg shells. The average diameter of an egg in a sample of ten from the general stock was 0.141 mm. The specific gravity of the eggs was $1.02 \pm$. Experiments were conducted at room temperature ($13.6^{\circ}\text{C}.$) in the laboratory. Measurements were made after eggs had been in a solution for thirty minutes; an average of ten being taken in each case. The results are shown in Table 2 and Figure 23.

Experiments were also tried in which eggs of about the same age were immersed in various solutions of sodium chloride. The results are given in Table 3 and Figure 23. Evidently the increase in diameter of eggs is due to the movement of water through the egg shell to balance unequal osmotic pressure, which results from the change in the external medium. In dilute solutions the relatively high concentrations of salt within the egg shell compared to the low concentration without was responsible for the inequality in pressure. In the concentrated solutions the activity coefficients of the dissolved salts were less than those within the egg shell and so even though the concentration was higher the water moved into the egg instead of from it. The behavior of larvae and adults in various solutions will be discussed later under salinity and chemicals.

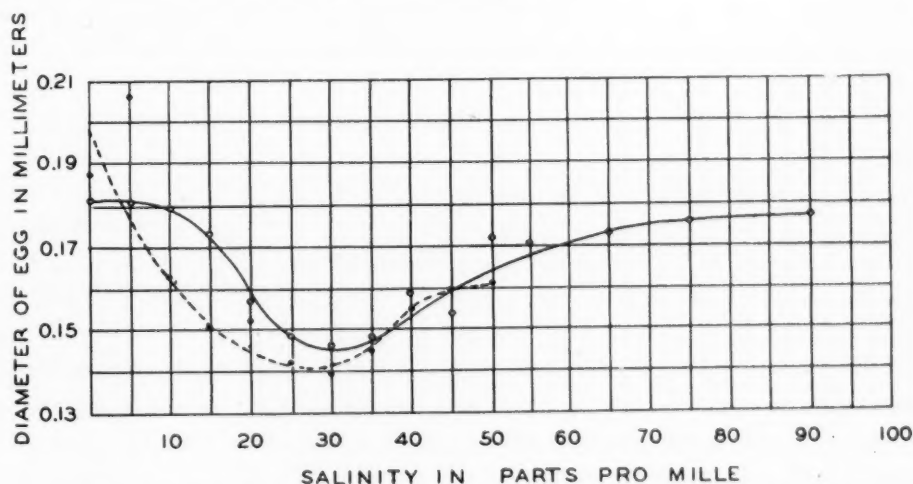


FIG. 23. Graphs showing size of eggs after being immersed for half an hour in sea water (-----) or in a sodium chloride (—) solution.

OXYGEN RELATIONS—Two methods were used in testing the rate of oxygen consumption of *Stylochi*. Some worms were tested in a Warburg apparatus. Others were kept separately in closed citrate bottles which had been filled with clean sea water and completely immersed. In containers in which water was kept without worms as a control measure there was no decrease in oxygen. The bottles used had a capacity of about 390 cc. Every 24 hours a bottle was removed and the oxygen content of the water was determined by the Winkler method. In sea water in the Warburg apparatus at 26.5°C. and in a salinity of 10 0/00 a *Stylochus* used 0.100 cc. of oxygen per gram of body weight per hour; at 26.5°C., S. 30, 0.108 cc. In citrate bottles at 26° ± C. and a salinity of 20 0/00 *Stylochi* consumed about 0.098 cc. per body gram per hour. Large individuals used oxygen more slowly than small. When the worms were left in closed citrate bottles they used progressively less oxygen after the second day, but never exhausted all the oxygen present while alive. When an individual died and decayed there was no oxygen present. Table 4 gives the amount of oxygen remaining after several days in citrate bottles in which *Stylochi* had been kept, and Figure 24 shows the computed rate of oxygen consumption in the bottles.

TABLE 4. AMOUNT OF OXYGEN REMAINING AFTER ONE EXPERIMENT IN WHICH TEN *Stylochus inimicus* HAD BEEN CONFINED IN CLOSED CITRATE BOTTLES FOR SEVERAL DAYS. THE WORMS RANGED IN VOLUME FROM 0.09 CC. TO 0.31 CC.

Days	1	4	6	7	8	9	10
O ₂ , cc. per l.	5.5	0.076	0.09	0.14	0.12	0.10	0.15
	0.13	0.13	0.12	0.16

DESICCATION—Adult *Stylochi* are able to endure considerable desiccation; the eggs and larvae, very little. Fifteen individuals were wiped on clean cheese cloth, weighed, and allowed to stand in open glass dishes for air drying, and again weighed. Eleven which lost from 18.2 to 54.6 percent of body weight lived when placed in sea water; four which lost from 57 to 66.7 percent died. When twenty *Stylochi* exposed separately in air in uncovered clean finger bowls in the laboratory where humidity was 72 to 77 percent and temperatures were 25.2 to 25.5°C. one individual lived eight hours. When twenty were exposed in clean dry, covered bowls at temperatures of 25.3 to 26.5°C. one individual revived when placed in sea water after an exposure of fifteen hours in air. Its margin sloughed off, but the worm regenerated its body and became practically normal without food in about a month. Another individual moved feebly after an exposure of twenty-four hours in air, but died in a couple of days after being placed in water. In air of 66 percent humidity at a temperature of 27.4°C. all *Stylochus* eggs survived an exposure of 35 minutes in open, dry finger bowls; only 2 out of 1,000 lived 40 to 85 minutes. Some experiments were tried in

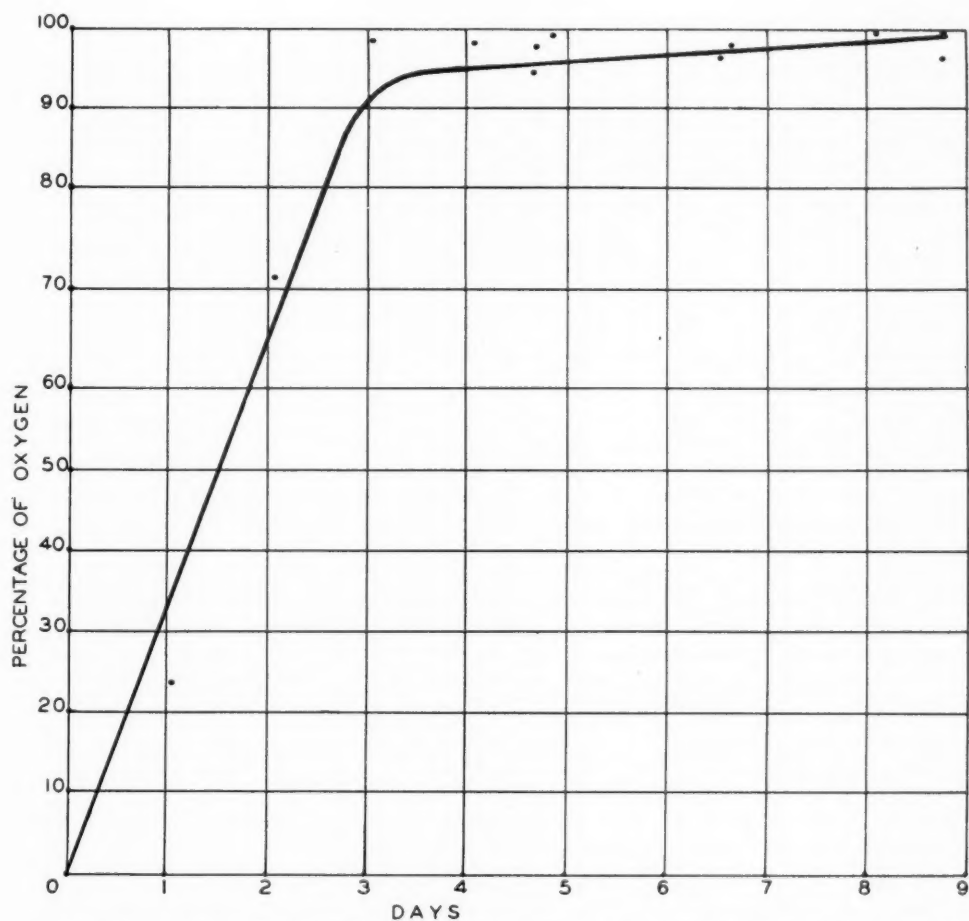


FIG. 24. Percentage of available oxygen consumed by *Stylochi* when left separately in sea water in closed citrate bottles. Volume of worms used ranged from 0.18 cc. to 0.31 cc.

which shell refuse was tonged up from oyster bars (Hagen's Flats; November 12, 3 P.M.), allowed to drain for a few minutes on the deck of a boat, and then placed in clean dry pails, which were placed outdoors where they were well protected from sun and wind. Water was added at twelve hour intervals to various pails; temperatures ranged between 12.5 and 20.4°C. Two living *Stylochi* were obtained from a pail in which shell refuse had been left without water for seventy-two hours. A similar test was made with pails tonged from East Hole on November 7; at temperatures of 17.4 to 23.6°C. living *Stylochi* were obtained when water was added to pails after forty-eight hours.

WATER CONTENT AND ASH—A *Stylochus* weighed about 0.222 grams per cubic centimeter. The ash from two lots of ten incinerated in an electric furnace was 2.1 and 2.4 percent of net weight (i.e.—weight after being wiped on cheese cloth). The percentage of dry weight after 18 hours in an oven at 36°C. was 23.8.

SALINITY—The general distribution of *Stylochus* on the oyster bars in Apalachicola Bay indicated that it flourishes best in rather high salinities. Observations in the laboratory support this view. Experiments were carried out in which *Stylochi* were transferred directly from sea water (S., 31.73 0/00) to various dilutions in finger bowls. Two worms were placed in each bowl and twelve were tested in each salinity. Under such conditions all of the worms died at salinities of 8 and 5 0/00 and most of them died at 11 0/00. However, when *Stylochi* were placed in pairs in finger bowls and transferred each day to gradually decreasing salinities some survived in dilutions of 6.42, 6.36, 6.07, and 5.88 0/00. Below 6 0/00 they curled and often failed to adhere to the substratum. Though *Stylochi* survived in rather low dilutions of sea water they usually did not lay eggs below salinities equal to about 15 grams per liter. Table 5 shows the number of eggs laid by *Stylochi* in various salinities. The number increases progressively from less to more salty dilutions of sea water.

TABLE 5. EGGS LAID BY EIGHTY *Stylochus inimicus* DURING TEN DAYS IN SEA WATER AND IN VARIOUS DILUTIONS; EIGHTY-ONE WORM IN SEPARATE FINGER BOWL; 23.1 C. TO 31.5 C. JULY TO AUGUST 10

Salinity	Number laying eggs	Average number eggs	Condition
4.90.....	0	0	Dead
8.19.....	0	0	Dead
11.31.....	0	0	Mostly dead
14.45.....	1	20 ²	Alive
17.76.....	6	403	Normal
20.95.....	8	1520	Normal
27.39.....	8	2112	Normal
33.87.....	7	2497	Normal

²Non-adherent and did not develop.

Stylochus larvae lived indefinitely when transferred directly from water having a salinity of 31-33.4 to 15.5 0/00. lived 45 minutes in 3.9; 10 minutes in 12.2; 7 minutes in 9.8; 3 minutes in 6.3; died at once and became opaque in 4.9 and 0.1 0/00.

Eustylochus meridianalis can tolerate lower salinities than *Stylochus inimicus*. In a pail of oyster shells and sea water collected from the north end of St. Vincent Bar February 17, and East Bay April 15 *Eustylochi* came to the surface and crawled about in salinities of 9.6 0/00; others were collected from pails in which salinities were 4.6, 3.2, 2.7, and 0.6 0/00. During January, when kept in finger bowls and subjected to gradually decreasing salinities four out of eight individuals lived in S. 2.93 0/00 for eight hours. When transferred directly from sea water (S. 32.2) to dilutions some lived in S. 6.44 0/00, but all died in S. 3.22 0/00. The swimming larvae of *Eustylochus*, when about 100 were transferred to dilutions, showed the following results after ten minutes: S. 30 to 15, normal; S. 10, about half dead; S. 9, several alive; S. 8, 7, few alive; S. 6, 5, 0, all dead.

Mr. C. F. von Herrman, United States Weather Bureau, has kindly furnished data for rainfall in Georgia and for the height of the Apalachicola River at Blountstown. His report (Climatological Data, Georgia Section 35:51) says "the year 1931 was thus the driest on the records for the past 40 years." This was followed by a great epidemic of oyster "leeches" in Apalachicola Bay during the following year (1932). Dr. H. F. Prytherch has constructed a graph which shows mean monthly river heights at Blountstown, Florida, from 1931 to 1934. His observations show that there have been more *Stylochi* in Apalachicola Bay during periods of drought.

CHEMICALS—In the hope that some chemical might be found which would be of value for killing oyster "leeches" twenty-five substances were tested in sea water during August, September, and October. The following list gives the lowest concentration which killed adult *Stylochi*:

0.001 percent—Beta naphthylamine.

0.01 percent—Potassium cyanide, sulfuric acid, shirlan N. A., Dupont shirlan D., para cresol, sodium hypochlorate.

0.1 percent—Sodium hydrate, potassium hydrate, hydrochloric acid, nitric acid, acetic acid, phenol, ortho nitro phenol, furfural.

1.0 percent—Ethylene chloride.

Saturated—Nitro benzene, brom benzene, naphthionic acid 1-4, Dupont shirlan crude, beta naphthylamine.

A 1.0 percent solution of sodium fluoride and a saturated solution of naphthelene had no apparent effect. Experiments with *Stylochus* larvae gave the following lowest concentrations which caused death:

0.001 percent—Copper sulfate, sodium hypochlorate.

0.01 percent—Potassium hydroxide, sodium hydroxide, beta naphthylamine, para cresol, shirlan, shirlan D.

0.1 percent—Hydrochloric acid, sodium fluoride, furfural, ethylene chloride, brom benzene, ortho nitro phenol.

Saturated solution—Nitro benzene (10%), naphthionic acid 1-4. In solution of some of the substances tested adult worms died variously. Sometimes a very strong solution caused the body to curl up tightly and stiffen without the secretion of mucus; whereas a weaker solution caused strong contraction, so that internal parts were squirted out through the integument, crinkling of margins, and abundant secretion of mucus.

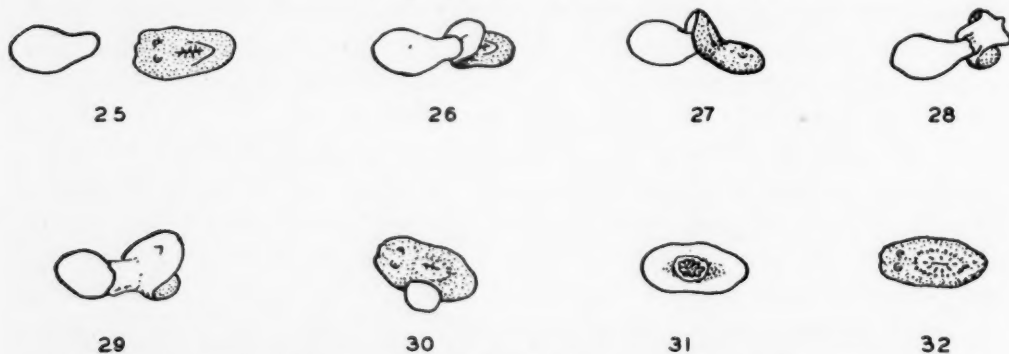
TEMPERATURE—The limits of toleration of *Stylochi* for high temperatures were tested by slowly heating five individuals in a beaker containing 300 cc. of sea water which was stirred constantly on a sand bath. Up to 40°C. all lived; at 41°C. two died and three lived; at 42°C. all died. Low temperatures were tested in an electric refrigerator where by shifting to different regions various temperatures could be maintained fairly constant for hours at a time. The worms were placed separately in ten 100 cc. beakers filled with sea water; a pair of beakers could thus be removed at

intervals. Individuals recovered after being kept at 1.0, 0.7°, and 0.5°C. for one hour or more but all those that reached 0.0°C. or below died. Larvae survived lower temperatures than adults. Some lived for more than an hour at -2.0°C.; about a twentieth of those subjected to -2.5°C. were alive, though the water about them contained ice crystals.

Adult *Eustylochus meridianalis* tolerate lower temperatures than *Stylochus inimicus*. At 9.16°C. to 11.3°C. the latter crumpled up and lost its attachment to the substratum while the former continued to crawl about and remained attached down to -1.0°C. *Eustylochus* adults lived in ice at -2.0°C.; larvae survived -1.0°C. Adult *Eustylochus* usually died when heated to 39.0°C.; e.g.—in one experiment 2 of 5 lived after five minutes at that temperature, but after ten minutes five others all died. At 40.0°C. all adults tested died. *Eustylochus* larvae survived temperatures as high as 44.0°C. for a short time and recovered.

In order to test the effects of temperature on egg-laying two lots of ten pairs of *Stylochus* in separate covered finger bowls were kept under different conditions from November 18 to 28. Lot 1 was kept in the laboratory where temperatures ranged from 8.3 to 25.7°C., average 18.7°C.; after ten days all "leeches" were alive, 12,800 eggs had been laid in three bowls. Lot 2 was kept on the north porch of the laboratory, where temperatures ranged from 3.3°C. to 21.9°C., average 13.9°C.; after ten days 13 were alive and 7 dead, no eggs had been laid.

FOOD AND FEEDING—*Stylochus inimicus* apparently feeds largely on oysters (Figs. 25-32). In the laboratory individuals which had not had food for some time ate the soft parts of barnacles and crepidulas, but did not eat shrimp or fish. On the other hand *Eustylochus meridianalis* readily ate barnacles and even killed *Balanus* to get food, but was never seen to enter a living oyster to feed on it, though it was given many opportunities to do so. *Stylochi* which had just been brought in from the field were teased apart in attempts to discover the nature of the foods eaten. Nothing was found but parts of oysters, except a very few small organisms, such as peridinians and



FIGS. 25-32. A *Stylochus* approaching (25) a piece of oyster, swallowing it (26-30), withdrawing its pharynx (31), and engorged (32).

diatoms, which were probably part of the food of the oysters eaten. *Eustylochi* kept without food from March 20 to April 2 decreased from an average length of 14.0 mm. to 10.5 mm. (25 percent) during the thirteen days. *Stylochi* kept without food from November 18 to March 5 decreased from an average length of 24.2 mm. to 16.6 mm. (30 percent).

BEHAVIOR—When placed in a rectangular glass dish containing sea water in a dark room adult *Stylochi* are generally negative to a horizontal beam of light of intensity of about 0.15 to 3.5 candle meters. Larvae were strongly positive under similar conditions. Adults appear to move without reference to currents. Swimming larvae are somewhat negatively rheotropic; e.g., in current moving at a rate of 10 mm. per second the larvae swam in an erratic course with many twistings and turnings, but only moved along with the current at a rate of about 8.8 mm. per second. The tentacles and brain of adults are not essential to photic and rheotic responses; animals respond more slowly but in much the same way after these organs are removed. Most individuals are strongly stereotropic and if dislodged will usually turn over repeatedly so as to keep the ventrum in contact with the substratum. The brooding responses when eggs are present have already been discussed. They are probably brought about by chemico-tactile stimuli.

ECOLOGY

Stylochus inimicus in its environmental relations requires food, which appears to consist largely of the fleshy parts of oysters; sea water in which salinity does not fall below about 6 ‰ and for as much as a fortnight remains above about 15 ‰ for the development of eggs; temperatures above about 10°C.; clean shells or other similar objects, which are not already occupied by annelids, crabs, alpheidids, sponges, clams, snails, barnacles, or other animals, for shelter and the deposition of eggs. Such a complex of environmental conditions is most often found on oyster beds in comparatively warm climates. As oysters usually grow in estuaries where water is brackish and at times becomes too fresh for the reproduction, or even the life of *Stylochus*, there is at times antagonism between requirements for food and those for propagation. *Eustylochus meridianalis*, though it is often associated with *Stylochus*, lives in a somewhat different environment where acorn barnacles may constitute the chief food, where water may be fresher (0.6 ± 0 ‰) and temperatures lower. As would be expected *Stylochus* is found primarily on oyster beds along the southern coasts of Florida, on both the east and west coasts; *Eustylochus* is known to range from Maryland to Texas and is widely distributed on oyster beds, piles, isolated old shells, logs, and other similar situations.

DISTRIBUTION—Two methods were used in studying the distribution of polyclads in Apalachicola Bay and adjacent waters: (1) A measured bushel of tonged oysters and shells was carefully searched by Pearse, Wharton, Saw-

yer and Lane; nearly every living and dead shell was opened and scrutinized, inside and out—barnacles, crepidulas, mussels, etc.; all polyclads were counted, placed in a jar of sea water, and later measured in the laboratory; records were also kept of numbers of individuals (a) in or on clean oyster shells, (b) in living or recently dead oysters, and (c) those brooding clutches of eggs, and at times the number of eggs in clutches. (2) A fifth of a bushel of oysters was placed in a white enameled pail and covered with water. The pails were taken to the laboratory and allowed to stand for 24 or 48 hours, depending on temperature; the polyclads which came to the surface were removed, counted, and measured. When salinities were low those in pails were determined by titration with silver nitrate. From August 8 to November 19, 1935 the shells put into pails were those which had already been searched in examining bushels, in order to ascertain whether the bushel-searching methods were effective, but from November 25, 1935 to May 20, 1936 unexamined shells only were used for the pail survey method. Of course smaller polyclads, even swimming larvae, could be found than on the clean shells in the field. After much preliminary scouting fifteen stations (Fig. 33) which represented conditions on various types of oyster beds were selected for study, and were visited at least once each month after June 20, 1935. In the following list depths given are the means from which oysters were actually tonged or (Hile's Deep Bar only) dredged; s indicates surface; b, bottom:

1. Hile's Shallow Bar, near Indian Pass, an oyster bed planted with dredged oysters from East Hole and Cat Point in 1931-1932; mean depth 1.3 meters; salinity, s, 32.45-5.97, b, 34.41-5.97; temp., s, 25.6-12.0°C., b, 32.0-12.0°C.
2. Hile's Deep Bar; an artificial bed planted with dredged oysters from East Hole and Cat Point in 1931; depth 3.4 meters; salinity s, 33.88-2.34, b, 34.02-8.50; temp., s, 28.9-11.4°C, b, 28.9-10.6°C.
3. Picolyn Bar; a natural oyster bed which has been tonged for many years, but never dredged; depth 1.1 meters; salinity s, 33.75-2.74, b, 33.75-3.04; temp., s, 28.5-11.2°C., b, 32.3-11.6°C.
4. Lump off 11-Mile; a natural bed where oysters have long been tonged, but never dredged; depth 1.2 meters; salinity s, 32.28-1.60, b, 33.85-1.60; temp., s, 29.9-7.7°C., b, 31.1-7.7°C.
5. Big Bayou Bar; a bed in a lagoon on the north side of St. Vincent Island which contains some native oysters, but mostly planted with oysters from East Hole and Cat Point in 1933; depth 1.7 meters; salinity s, 30.07-2.31, b, 29.80-24.7; temp., s, 30.4-11.4°C., b, 30.4-11.4°C.
6. St. Vincent Bar, North End; a natural bar which has long been exploited by tongs, and since 1933 by dredges; depth 1.5 meters; salinity s, 32.46-0.40, b, 34.58-0.60; temp., s, 27.8-7.2°C., b, 31.4-4.2°C.
7. St. Vincent Bar, Middle; depth 1.4 meters; salinity s, 32.46-1.90, b, 33.35-1.90; temp., s, 28.3-8.1°C., b, 32.0-8.1°C.
8. St. Vincent Bar, South End; depth 1.4 meters; salinity, s, 32.47-1.60, b, 35.16-2.52; temp., s, 27.8-7.2°C., b, 29.9-7.2°C.

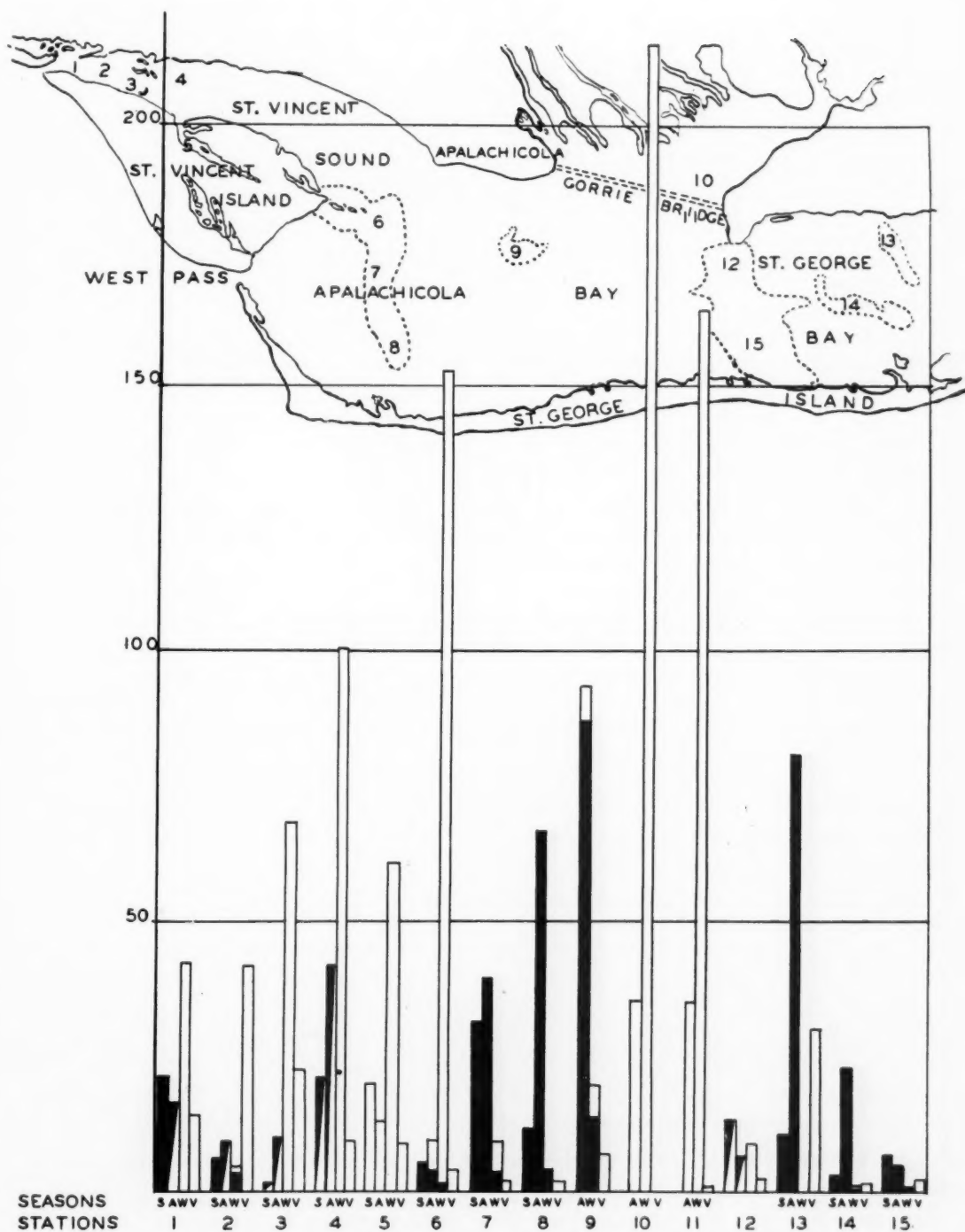


FIG. 33. Stations in Apalachicola Bay where monthly observations were made. Black indicates seasonal distribution of *Stylochus inimicus*; white, that of *Eustylochus meridionalis*. Seasons: A, autumn; September, October, November; S, summer; June, July, August; V, spring; March, April; W, winter; December, January, February. Based on Table 6.

9. Hagen's Flats; a natural bar which has been tonged and dredged; depth 1.8 meters; salinity s, 30.96-0.50, b, 31.14-2.20; temp., s, 24.4-9.2°C., b, 24.6-9.2°C.

10. East Bay; a natural oyster bed which has been tonged and, since 1933, dredged; depth 1.9 meters; salinity s, 20.19-0.00, b, 28.66-0.10; temp., s, 28.2-8.9°C., b, 28.2-8.9°C.

11. Gorrie Bridge, East End; a natural bar which has been tonged and dredged; depth 1.6 meters; salinity s, 29.51-0.05, b, 29.37-0.05; temp., s, 28.4-9.6°C., b, 28.3-9.4°C.

12. Cat Point; a natural oyster bed which has been tonged and dredged; depth 1.6 meters; salinity s, 31.69-0.05, b, 31.92-0.05; temp., s, 26.7-8.9°C., b, 31.7-8.9°C.

13. Porter's Bar; a natural oyster bed which has been tonged and dredged; depth 1.6 meters; salinity s, 31.98-2.35, b, 31.98-3.96; temp., s, 23.9-8.6°C., b, 32.2-8.6°C.

14. Platform Bar; a natural oyster bed on which "leeches" were abundant in 1932; tonged and dredged; depth 1.6 meters; salinity s, 32.23-2.03, b, 32.23-3.23; temp., s, 23.9-8.9°C., b, 32.7-8.9°C.

15. East Hole; a natural bed, near St. George's Island, which has been tonged and dredged; depth 2.1 meters; salinity s, 31.98-2.23, b, 32.23-3.02; temp., s, 37.0-8.6°C., b, 32.2-8.6°C.

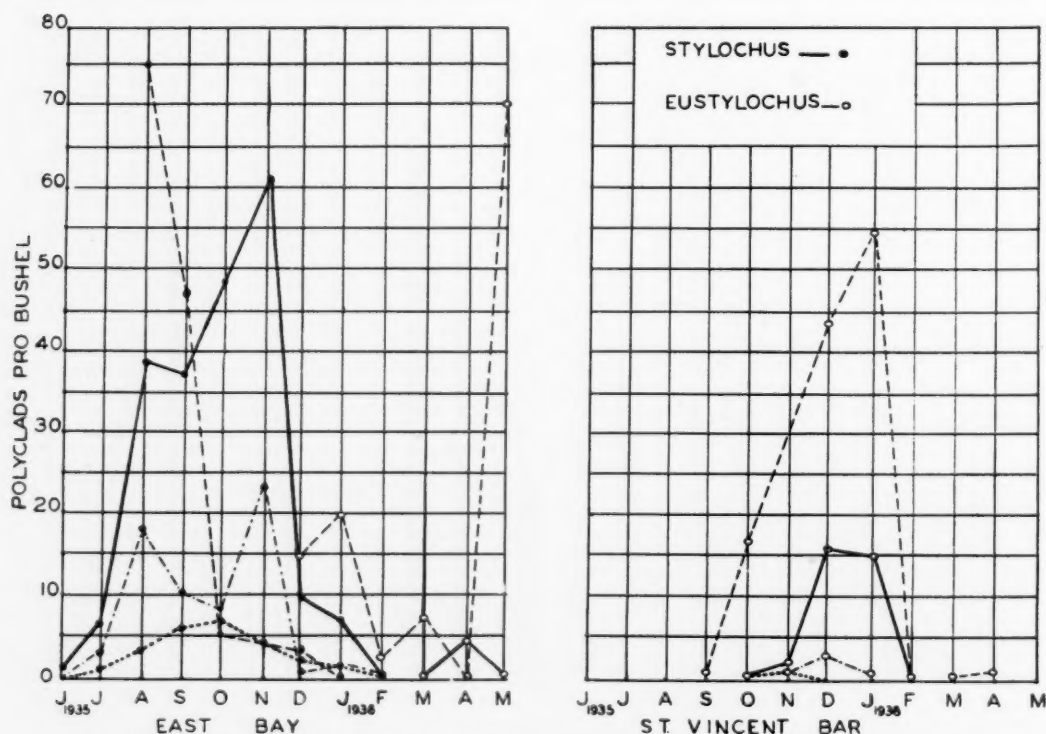


FIG. 34. Seasonal distribution of *Stylochus* and *Eustylochus* in the middle of St. Vincent Bar and in East Bay, showing numbers found in pails (-----), in bushels (—), in live oysters (.....), and with eggs (-.-.-). *Eustylochi* taken in pails from East Bay are shown as numbers in one tenth of a bushel; those from St. Vincent Bar in number per bushel.

The numbers of *Stylochus* and *Eustylochus* at the fifteen stations studied is shown throughout a year in Figure 33 and Table 6.

TABLE 6. *STYLOCHUS* AND *EUSTYLOCHUS*; DISTRIBUTION BY SEASONS
JUNE, 1935 TO MAY, 1936

Figures indicate polyclads per bushel

Station	SUMMER		FALL		WINTER		SPRING	
	June-August		September-November		December-February		March-April	
	<i>Stylochus</i>	<i>Eustylochus</i>	<i>Stylochus</i>	<i>Eustylochus</i>	<i>Stylochus</i>	<i>Eustylochus</i>	<i>Stylochus</i>	<i>Eustylochus</i>
1. Hile's Shallow Bar.....	20.8	0	15.8		5	37.9	0	13.9
2. Hile's Deep Bar.....	5.8	0	8.6		2.7	0.8	0	40.3
3. Picolina.....	0.8		8.7		0	67.8	0	21.8
4. 11-mile Lump.....	19.4		41.5		0	100.3	0	9.4
5. Bayou.....	0	20	0	12.9	0	61.7	0	8.8
6. St. Vincent's N.....	5.0	0	3.9	5.9	1.5	153.2	0	3.9
7. St. Vincent's M.....	30.3	0	39.6	0	3.3	6.3	0	1.4
8. St. Vincent's S.....	11.7	0	67.7	0	4	0	0	1.4
9. Hagen's Flats, inside.	—	—	86.5	7.5	13.7	5.8	0	7
10. East Bay, bridge								
outside.....	—	—	0	35.7	0	216.4	0	0
11. East Bay, bridge.....	—	—	0	35.6	0	169.0	0	.3
12. Cat Point.....	13.8		6.3		0	9.8	0	2.8
13. Porter's Bar.....	10.5	0	81	0	2	0	0	30.6
14. Platform Bar.....	3.2	0	23.3	0	0.8	0.4	0	1.4
15. East Hole.....	7.7	0	5.5	0	0.5	0	0	2.4

Stylochus reached its maximum abundance in the fall of 1935; *Eustylochus* was most abundant in the winter of 1935-36 and decreased greatly after the freshet early in the spring of 1936. *Eustylochus* continued to lay eggs when brought into the laboratory throughout the winter and spring. In general, *Stylochus* flourished during warm weather where oyster beds grew in rather salty water; *Eustylochus* was more often found during colder parts of the year where barnacles were abundant alongshore, on oyster beds or elsewhere. These statements are general and were of course not absolutely supported by field evidence. For example, the greatest number of *Stylochus* ever found in one "tonged and searched" bushel was 204 in October on Hagen's Flats, where water is not as salty as on St. Vincent Bar. The greatest number of *Eustylochus* per bushel by the pail method was 1375 on March 16 on Green Point lump, which is east of any of the stations studied in routine surveys. Water there is generally quite saline.

In any one season conditions in a particular place may be favorable or unfavorable. The millions of pelagic larvae which polyclads produce enable them to invade every available habitat; once established, fortunate or un-

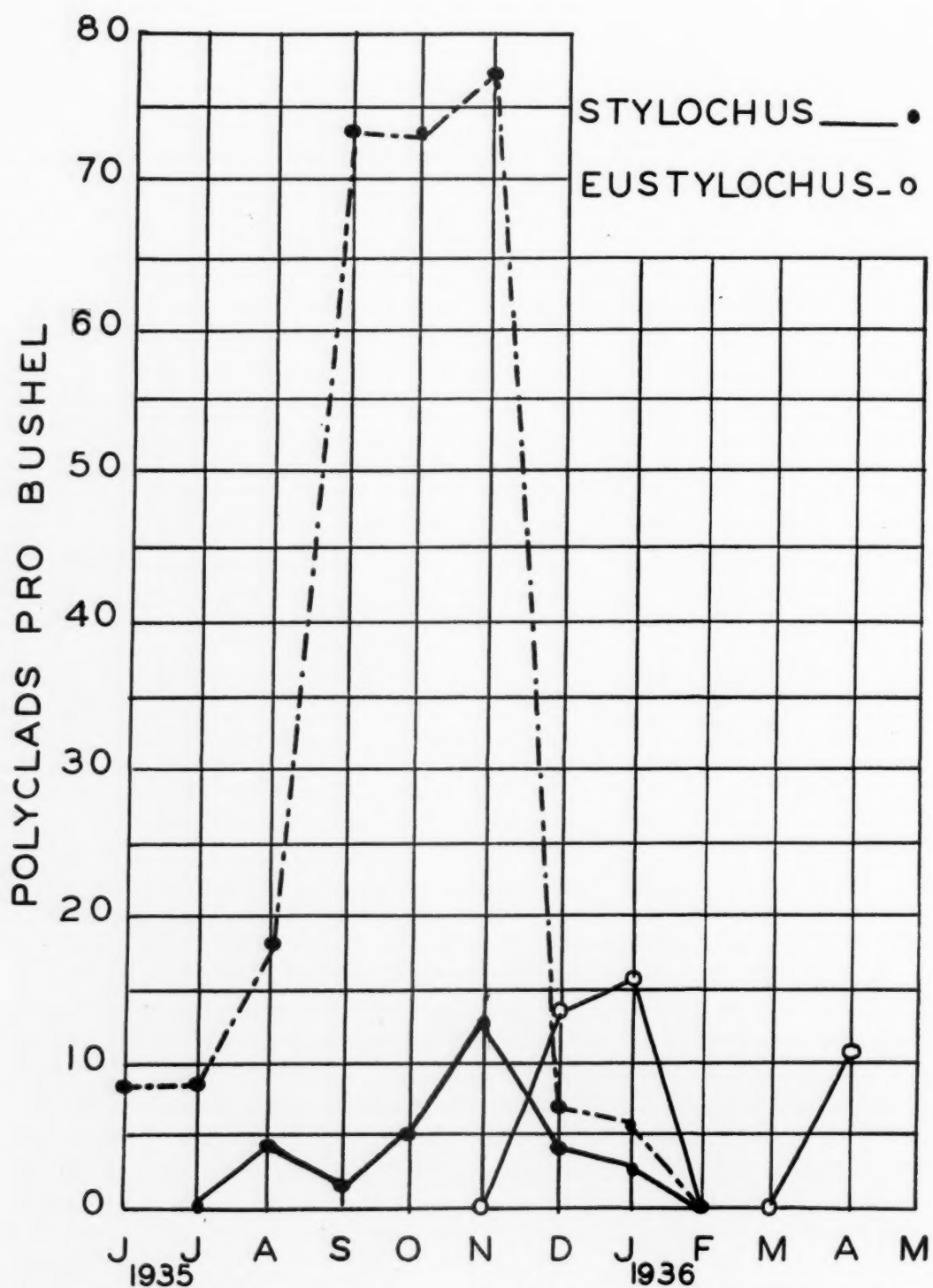


FIG. 35. Occurrence of *Stylochus* and *Eutylochus* per examined bushel, on the north (.....) and south (——) ends of St. Vincent Bar.

fortunate combinations of winds, freshets, temperatures, and other environmental factors determine whether they perish, survive, or flourish. In 1932-1935 there were myriads of *Stylochi* on Porter's Bar; in 1935-36 there were not as many there as on Hagen's Flats and St. Vincent Bar.

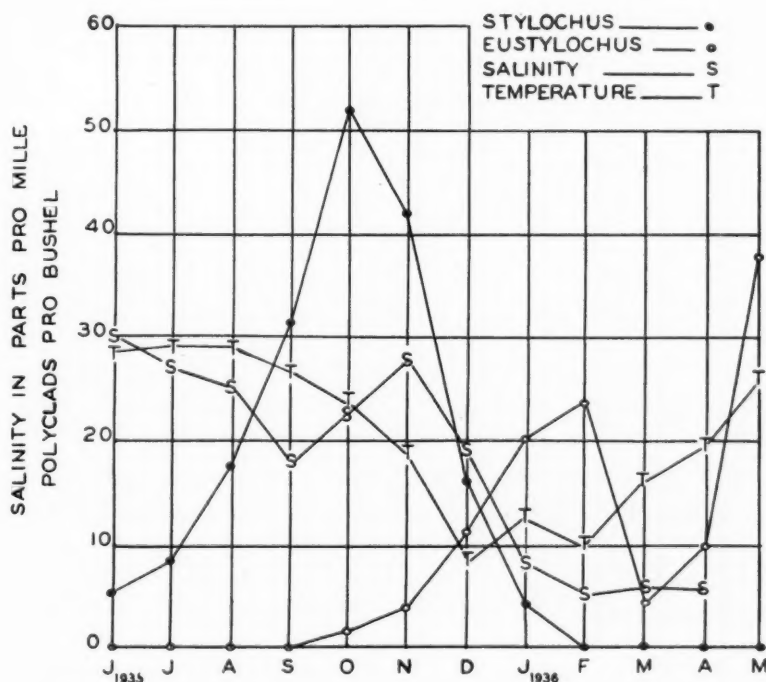


FIG. 36. Occurrence of *Stylochus inimicus* and *Eustylochus meridionalis* in relation to salinity and temperature during 1935 and 1936 in Apalachicola Bay.

Foods—Polyclads appear to have become specialized for particular types of food: *Stylochoplana floridana* Pearse eats copepods and annelids; *Thysanozoon brochii* Grube commonly feeds on the ascidian, *Didemnum candidum* Savigny, which grows on the eel grass in St. Joe Bay. *Stylochus inimicus* apparently feeds on oysters, and seldom on anything else. In the laboratory *Stylochi* which had been kept for some time without food ate acorn barnacles and crepidulas as well as oysters, but refused the flesh of fish, and several species of snails and clams. On October 28 four freshly collected oysters were put in an aquarium where there were about 1,000 *Stylochi* in running sea water. Three days later 85 of the worms had entered and were devouring one oyster; the three other oysters contained 21, 50, 51 worms. Table 7 indicates that young, small oysters are more often eaten than large. The "partitions" (Fig. 37) built as a defense against "leeches" are particularly significant in the table.

TABLE 7. SHOWING ATTACKS OF TEN *Stylochus inimicus* ON FRESH OYSTERS FROM CAT POINT. STYLOCHI INTRODUCED ON SEPTEMBER 9; TWO LOST BEFORE SEPTEMBER 16, WHEN OYSTERS WERE EXAMINED

Size of oysters, mm.	No. of oysters, Sept. 9	Stylochi in living oysters	"Leech" partitions in shells	Oysters rotting	Oysters dead	Oysters normal
1-10.....	177	..	8	4	46	131
11-20.....	84	2	2	..	8	74
21-30.....	8	..	1	1	2	6
31-40.....	5	1	1	4
41-50.....	1	1
51-60.....	9	9
61-70.....	6	1	5
71-80.....	3	3
81-90.....	8	1	..	2	2	5
Total.....	301	4	11	8	59	238

In the field *Stylochi* were often found in living, dying, or recently dead oysters, but, though thousands of crepidulas, acorn barnacles, and mussels growing with and attached to oysters were examined, none was ever found in them. *Eustylochus meridionalis* in the laboratory killed and devoured barnacles, readily ate the soft parts of barnacles and oysters, but was never observed to enter a living oyster, though it was given many opportunities to do so. In the field it was found in barnacles and oysters which were gaping open but never in closed, apparently healthy oysters.

ENTRANCE OF STYLOCHUS INTO OYSTERS—*Stylochus* was observed to enter living oysters on several occasions. The worm crept slowly up and attempted to enter between the lobes of the mantle. The oyster usually closed quickly and "blew" the leech out in the resulting current of water, but the leech persisted and usually after several trials succeeded in entering. But the oyster did not give up the struggle against its enemy. It at once began to secrete a horny partition and thus attempted to seal the worm into its own shell. In two instances *Stylochi* were found completely covered over in that way, and other instances were probably observed when the worms had disintegrated so that they could not be positively identified. In cases under observation it required about two days to build a partition. Sometimes the invading worm crept over the first defense partition that the oyster secreted and the oyster then made another; or at times even as many as five partitions. During such a struggle the oyster's body was confined to a smaller and smaller space; probably also weakened and perhaps partly devoured. The defensive partitions are such a characteristic response to *Stylochus* attacks that oystermen in looking over shells on bars or oyster shell refuse heaps remark, "leeches have been here," when they find such a partition. An oyster which has been invaded by a *Stylochus* opens and closes more often than one which has not been entered.



FIG. 37. Partitions built by oysters in attempt to keep Stylochi away from their bodies. *P*, partitions. *S*, a Stylochus behind a partition in a fresh oyster.

BREEDING—Any hard clean surface appears to be suitable for the reception of the irregular, single-layered egg masses of *Stylochus* and *Eustylochus*. The shells of molluscs are commonly used, but either worm will readily lay eggs on the sides of a glass dish. Temperature and salinity influence egg laying. When water is about half as saline as that in the open sea *Stylochus* lays few or no eggs. Egg laying is also inhibited by low temperatures. Therefore, an oyster "leech" may continue to live where it is not possible for it to reproduce. A *Stylochus* can move fast enough and lays a clutch of eggs quickly enough so that it could creep up several feet into the intertidal zone with a rising tide and leave eggs, but these would not survive as they have little ability to endure desiccation. However, *Stylochi* have a breeding period which extends over several months. During this time they appear to be ever ready to copulate and lay eggs when conditions are favorable, so it would be seldom that fresh water and low temperature would not be remitted for two or three weeks, so that eggs could be laid and hatched.

EFFECTS OF VARIATIONS IN ENVIRONMENT—*Stylochus inimicus* and *Eustylochus meridionalis* are members of complex societies which live on oyster beds. Perhaps it is correct to say that the latter belongs to the *Balanus* Society rather than the *Ostrea* Society, and that it spreads over oyster beds when conditions are particularly favorable. The plants and animals which form societies fluctuate in numbers greatly in different years and with changing seasons in any one year. The most apparent causes of fluctuations in Apalachicola Bay are changes in salinity and temperature. In the summer and autumn of 1936 the following plants and animals lived together on the oyster beds in the bay. In the list which follows *S* indicates salinity in grams per liter. Of course the list does not include all animals which occur in Apalachicola Bay and adjacent waters, but only those that were encountered on oyster beds or appeared to be significant in the study of oyster leeches. As the animals have been identified by specialists, their names are given with brief notes which may be of use to those who work in the region. Unless otherwise stated the notes refer to collections made during routine monthly visits to the fifteen oyster bars selected for study (p. 626).

LIST OF PLANTS AND ANIMALS

Observed on Oyster Bars in Apalachicola Bay

PROTOPHYTA

Ulva sp.

Sea lettuce was often encountered in the east end of Apalachicola Bay; on such bars as North Lump and Sugar Loaf.

Sargassum natans (L.) Meyen

This alga was collected on June 6 on Platform Bar and on March 16 on North Lump.

Gracilaria confervoides (L.) Grev.

This branching alga was common to abundant throughout the year on Platform Bar (S: Bl. 98-3.23), East Hole, Porter's Bar, North Lump, and Sugar Loaf. At times it constituted an obstacle to tonging and dredging operations.

Spirogyra sp.

Collected in East Bay February 6 (S:0.1) after a freshet.

Enteromorpha intestinalis (L.) Link.

East Hole, December 30; S: 14.94.

Enteromorpha prolifera Agardh.

March 16; Sugar Loaf; S: 22.30.

PROTOZOA

Nematopsis ostrca Prytherch

Living oysters were sent to Dr. H. F. Prytherch from 11-mile Lump and Platform Bar on December 27 and December 30. Spores of this sporozoan parasite were found in the gills: from 400 to 25,000 per square centimeter. In 1934 Dr. Prytherch found this sporozoan in oysters collected in Apalachicola Bay from Bulkhead Bar. Oysters sent by the writers from Fernandina and Oslo on the east coast of Florida at the end of January were also found to contain spores by Dr. Prytherch.

PARAMECIUM, COLPODA, OXYTRICHA

On February 6 in pails of oyster shells collected from East Bay (S:0.1) numerous ciliates collected at the surface.

PORIFERA

Cliona vastifica

The boring sponge was most commonly found attacking oysters in the parts of Apalachicola where salinities were high—Platform Bar, Porter's Bar, St. Vincent Bar, Hile's Deep Bed, Picolyne Bar. Sponges were not common in the bay.

COELENTERATA

Nemopsis bachei Agassiz

In tow nets at East Hole (S:14.94) December 30; Picolyne Bar (S: 22.47) and Hile's Shallow Bed (S: 23.81), January 2; and Hagen's Flats (S:17.24), January 9.

Physalia pelagica Bosc

The Portuguese-man-o'-war was at times common on the beaches along the outlets but was never seen in Apalachicola Bay.

Stomolophus meleagris Agassiz

Rhizostomes were often swept into Apalachicola Bay on currents from the Gulf of Mexico.

Renilla reniformis (Pallas)

This stalked actinian was commonly in shrimp trawls in the Gulf of Mexico just off shore, but was not observed in Apalachicola Bay.

Paranthus rapiformis (Lesueur)

This anemone was common in the sandy shores of Indian Pass, and was the species often found on oyster shells in Apalachicola Bay where salinities were rather high, but specimens of the latter were too young to be identified with certainty.

Astrangia danae Edw. & Haime

This coral was found among tonged oysters on St. Vincent Bar and Platform Bar. No living specimens were found after the freshet in the winter of 1935-36.

CTENOPHORA

Mnemiopsis gardeni Agassiz

Ctenophores were captured in tow nets at various times and places: December 6, East Bay (S:18.73), Hagen's Flats (S:14.66); January 2, Big Bayou Bar (S:19.76); January 9, East end of Gorrie Bridge (S:14.45).

PLATYHELMINTHA

Stylochus inimicus Palombi

The oyster leech was distributed throughout Apalachicola Bay and adjacent areas until the freshets in January, February, and March destroyed it.

Stylochus floridanus Pearse

Seven specimens were collected during the summer from the oyster beds in Apalachicola Bay.

Eustylochus meridionalis Pearse

This polyclad is usually associated with barnacles, but is often found on oyster beds and eats oysters at times. It tolerates lower salinities and temperatures than local representatives of the genus *Stylochus*.

Hoploplana thaisana Pearse

This polyclad was found several times during the autumn. When crushed conchs (*Thais* f. *floridana* Conrad) were allowed to stand in dishes of sea water, the worms crept up around the edge.

Acerosita pellucida Pearse

Two specimens of this polyclad were found on St. Vincent Bar in June.

Oculoplana whartoni Pearse

This ribbon-like polyclad was found on oyster shells in Apalachicola Bay, and at Crystal River and St. Lucie, Florida.

Prosthlostomum lobatum Pearse

This slender, flat polyclad was found several times on oyster beds in Apalachicola Bay, and is widely distributed elsewhere in Florida on both east and west coasts.

Bucephalus gracilescens (Rudolphi)

This trematode was found infesting oysters on the beds in Apalachicola Bay: June 23, St. Vincent Bar; January 9, East Bay; January 22, Platform Bar and East Hole; January 24, Picolyn Bar; January 24, Big Bayou; February 14, Cat Point.

ANNELIDA

Phyllodoce n. sp.

This annelid was found on St. Vincent Bar during the summer and autumn when salinities were rather high, and in St. Joe Bay on October 24.

Harmothoe aculeata Andrews

This worm was found on Picolyn Bar on November 18; and in Crooked Island Sound on November 21.

Lepidametria commensalis Webster

This polynoid occurred on St. Vincent Bar during June and July, and was found on Picolyn Bar August 10.

Euphole globosa Winternitz

St. Vincent Bar, July 5, 1935.

Eusyllus sp.

St. Vincent Bar, June 5.

Autolytus n. sp.

St. Vincent Bar, September 26.

Podarke obscura Verrill

St. Vincent Bar, August 1.

Nereis limbata Ehlers

This was the commonest and most widely distributed polychaete on the oyster beds in Apalachicola Bay at all seasons ($S: 34.74-0.05$). It lived among oyster shells everywhere. At times it was found in live oysters, which built partitions in attempts to shut it out of the mantle cavity.

Nereis pelagica L.

This worm was not as common as the last and did not tolerate as low salinities, but regularly lived among oysters in Apalachicola Bay.

Marphysa acicularum Webster *brevibranchiata* Treadwell

Hile's Shallow Bed; July 11.

Glycera sp.

St. Vincent Bar, July 19.

Polydora sp.

This worm was twice found moving about in living oysters (December 3, St. Vincent Bar; March 30, Big Bayou Bar) and was commonly found in holes along the margins of the shells of living oysters. It apparently bores into the shell of the oyster and doubtless does some damage. Oysters often cover the worms over with secretions and thus imbed them in their shells. *Polydora ciliata* (Johnson) infests shells of oysters in New South Wales.

Chaetopterus variopedatus Revieri

In beaches at Indian Pass and on the flats in St. Joe Bay, but not found on the oyster beds in Apalachicola Bay.

Streblosoma verrilli Treadwell

Porter's Bar, December 30, March 4; St. Vincent Bar, June 5, July 5, July 19, December 27.

Eupomatus uncinatus (Phil.)

Commonly distributed throughout Apalachicola Bay on oyster shells and other suitable objects.

Thalassema mellita Conn.

St. Vincent Bar, July 5.

ROTIFERA

Rotifers were taken in tow nets on Picolyne Bar, January 2, and in East Bay, March 6.

ECHINODERMATA

Hemipholis elongata (Say)

The young of this ophiuroid were the only echinoderms found on the oyster beds in Apalachicola Bay, but in St. Joe Bay and Crooked Island Sound, only a few miles to the east, there were ten other species. *Hemipholis* was not found where the lowest salinities obtained.

ARTHROPODA

CRUSTACEA

COPEPODIDA

Echinostoma curticorne Boeck

This crustacean came to the surface in a pail of oyster shells collected on St. Vincent Bar, June 12.

Mytilicola intestinalis Steuer

A specimen of this copepod was taken from a living oyster which was collected on Hagen's Flats December 5. Dr. C. B. Wilson, who identified it, writes that it has not been taken in America before.

CIRRIPEDIDA

Balanus cburneus Gould

This acorn barnacle was the commonest one throughout Apalachicola Bay at all seasons (S: 33.27-0.05). At the end of March many individuals were with eggs. Though this barnacle was most abundant on oyster shells in brackish water, most of the small individuals in East Bay died after the freshets in February and March, when salinities went as low as 0.05 0/00, but some large individuals survived.

Balanus improvisus Darwin

This barnacle was not as common in Apalachicola Bay as the last, but was also widely distributed.

AMPHIPODIDA

Gitanopsis tortugae Showmaker

A small amphipod which was present throughout Apalachicola Bay from Platform Bar to Indian Pass during the summer, but was not seen after the freshets in the winter.

Melita nitida Smith

This amphipod was distributed throughout Apalachicola Bay on the oyster beds. It survived the winter freshets and in April persisted in salinities as low as 0.05 0/00 in East Bay.

Carinogammarus mucronatus (Say)

This amphipod appeared in East Bay in February after freshets and during March and April spread to St. Vincent, Porter's, Platform, and East Hole Bars.

Grubia compta (Smith)

Found in the east end of Apalachicola Bay, East Hole, Platform Bar, and Cat Point from June to late in January; also in Crooked Island Sound, January 22.

Corophium simile Shoemaker

East Bay; April 13, (S: 0.05).

Corophium acheruscium Costa

11-mile Lump; November 19.

Grandidierella megnae (Giles)

Distributed throughout Apalachicola Bay, at times in very low salinities, from July to April.

Caprella acutifrons Latreille

Platform Bar; June 6.

Caprella linearis L.

St. Vincent Bar, September 26; St. Joe Bay, March 11.

ISOPODIDA

Leptochelia dubia (Kr)

Cat Point, Porter's Bar; January 22; Porter's Bar (S:12.73), East Hole (S:3.02), April 15; St. Vincent Bar (S:3.20), April 17. In the eastern end of Apalachicola Bay this isopod was common August to April.

Exoxphacroma faxoni Richardson

Platform Bar, June 6; East Hole, January 22.

Erichsonella attenuata (Harger)

Platform Bar, June 6.

Erichsonella filiformis (Say)

East Hole, January 22.

Pseudione curtata Richardson

In the gill cavity of *Petrolisthes armatus* (Gibbes) throughout the summer.

DECAPODIDA

Palaemonetes vulgaris (Say)

Platform Bar, Porter's Bar, June 6; St. Vincent Bar, July 2.

Palaemonetes carolinus Stimpson

Cat Point; August 27.

Penaeus setiferus (L)

Common at certain seasons in Apalachicola Bay, especially in spring, and caught in trawls.

Crangon armillatus (M. Edw.)

Distributed on oyster beds throughout Apalachicola Bay; June to April.

Petrolisthes armatus (Gibbes)

This porcellanid was common among oysters on the beds in Apalachicola Bay during the summer and autumn, but was killed out by the winter freshets and none was seen after January 24.

Paguristes puncticeps Milne-Edwards

This large hermit crab continually wandered over the oyster beds and beaches of Apalachicola Bay, but on some of the former it succumbed to the winter freshets.

Hepatus epitheliticus (L.)

Hile's Deep Bed, July 11.

Callinectes sapidus Rathbun

The blue crab is common throughout Apalachicola Bay and persisting in salinities as low as 0.05 0/00; in winter it is buried in the bottoms and hard to find. Females with eggs were observed March 30.

Hexapanopeus augustifrons (Benedict & Rathbun)

Platform Bar, June 6.

Panopeus herbstii stimpsoni Rathbun

This crab was fairly common on the oyster beds in Apalachicola Bay, from June until the freshets in the winter killed it. None was seen on the beds after January 9.

Eurypanopeus depressus (Smith)

This little xanthid crab was abundant at all seasons throughout Apalachicola Bay and persisted on the oyster beds when salinities fell as low as 0.05 0/00.

Eurypanopeus dissimilis Benedict & Rathbun

Platform Bar; June 6.

Menippe mercenaria Say

The stone crab was common on oyster bars and alongshore in Apalachicola Bay. It persisted in salinities as low as 5.9 0/00.

Pinnotheres maculatus Say

Common in the wing shell, *Atrina rigida* Dillwyn, in Apalachicola Bay throughout the summer and until the host was killed by fresh water.

Pinnotheres moseri Rathbun

Hile's Deep Bed; November 19; one specimen was found in *Ostrea virginica* Gmelin.

Pinnotheres ostreum Say

On the east coast of Florida at Fernandina and Eau Gaillie, this crab was abundant in oysters; but at Oslo and St. Lucie it was rare, and was never seen by the writers on the west coast in or near Apalachicola Bay.

Pinnixa sayana Stimpson

One crab was found in the sand at Indian Pass, where *Chaetopterus* tubes were common; November 21.

Ocypode albicans Bosc

The ghost crab was common on the sandy beaches about Apalachicola Bay. In winter it was not active, but remained in the burrows.

ARACHNIDEA

ACARANIDA

Halacarid mites were taken on St. Vincent Bar, August 7; Picolyne Bar, August 21; in East Bay, January 9; and on Hagen's Flats, April 13.

ORIBATID MITE

Hagen's Flats, April 13, S:0.5.

INSECTEA

Enallagma sp.

At east end of Gorrie Bridge, Apalachicola Bay, February 6, S:0.6 nymph.

Hydroporus sp.

East Bay, February 6, S:0.1; April 13, S:0.05.

Helodid beetle larva

East Bay; February 6; S:0.05.

Rhagovelia sp.

One female was collected at Cat Point August 27, S:15.30-21.73.

Culex restuans Theobald

One larva was captured in East Bay, February 6, S:0.1-0.2.

Chironomus sp.

The larvae of this chironomid were common in East Bay February 6 to April 14, S:0.05-2.39; and at Cat Point, April 15, S:3.63.

Palkomyia sp.

Two larvae were taken in East Bay, March 6, S:2.36.

Protenthes culiciformis L.

Larvae were collected among living oysters in East Bay, April 13, S:0.05.

Orthocladus sp.

Two larvae were collected among living oysters in East Bay, April 13, S:0.05.

MOLLUSCA

AMPHINEUREA

Acanthochites spiculosa Rue

This chiton was common in Crooked Island Sound and St. Joe Bay, but was collected only in the eastern end of Apalachicola Bay, on Porter's Bar, and East Hole Bar.

PELECYPODEA

Arca transversa Say

A few were taken on St. Vincent Bar throughout the summer.

Noctia ponderosa Say

St. Vincent Bar, June 12; Hile's Shallow Bed, July 11.

Atrina rigida Dillwyn

A few were collected on St. Vincent Bar, until all were killed by the winter freshets; Porter's Bar, August 9, December 30.

Ostrea virginica Gmelin

With the next species on bars throughout Apalachicola Bay; many died after the winter freshets, especially young individuals; those which had lived nearest the mouth of the river (East Bay) appeared to tolerate fresh water better than those (St. Vincent, Platform) nearest the open sea.

Ostrea equestris Say

With the preceding species throughout Apalachicola Bay, but generally in shallow water.

Lima hians Gmelin

St. Vincent Bar, June 5, July 2, 11; Hile's Shallow Bed, July 11.

Anomia simplex d'Orbigny

Common in St. Joe Bay and Crooked Island Sound; rare in east end of Apalachicola Bay.

Brachidontes recurvus Rafinesque

This mussel flourished throughout Apalachicola Bay and was abundant where water was rather fresh. After the freshets of the winter and spring of 1936, it showed little or no mortality in salinities as low as 0.05 0/00. It often grew in great clumps on oysters.

Brachidontes exustus L.

St. Vincent Bar, September 26; Crooked Island Sound, November 21.

Lithophaga bisulcata d'Orbigny

The "date shell" borer was found during the summer in oyster shells on St. Vincent and Porter's Bars. It bored in the shells of living oysters, but was not as common as *Martesia*.

Pinctada radiata Leach

This clam was taken June 5 and 14 on St. Vincent Bar.

Chama macerophylla Gmelin

St. Vincent Bar, June 12; Hile's Shallow Bar, July 11.

Trachycardium muricatum L.

St. Vincent Bar, June 3; Hile's Shallow Bar, July 11.

Chione cancellata L.

St. Vincent Bar, June 5, July 11; Hile's Shallow Bed, July 11; Hile's Deep Bed, March 2; Crooked Island Sound, November 21.

Venus mercenaria L.

St. Vincent Bar, June 14; Hagen's Flats; April 13, S:2.63.

Semele proficula Pult

St. Vincent Bar, June 5, 12; Hile's Shallow Bed, July 11.

Corbula blattiana C. B. Adams

St. Vincent Bar, June 25, July 2, 19; Hile's Shallow Bed, July 11.

Martesia cuneimeris Say

This little pholid bored into the shells of living oysters on most of the bars in the more saline waters of Apalachicola Bay. It was recorded from the following bars: St. Vincent, Paradise, Platform, Porter's, Hile's Deep, Hile's Shallow, Cat Point, Big Bayou, 11-mile, Picolyn, North Lump, and Sugar Loaf. Often the burrows of the clams penetrated completely through the shell and were sealed over by the oyster's mantle on the inside. This borer was killed by the freshets on St. Vincent Bar.

GASTROPODEA

Diadora alternata Say

St. Vincent Bar, June 12, 25, July 2; common in St. Joe Bay.

Turbonilla sp.

St. Vincent Bar, September 26.

Odiostomia impressa Say

St. Vincent Bar, August 1, September 26.

Polinices duplicata Say

St. Vincent Bar, June 12, October 10; Hile's Deep Bed, January 24; Crooked Island Sound, February 10.

Crepidula plana Say

This flat snail was abundant on old shells and those of living oysters in Apalachicola Bay. It was not found where waters were of low salinity (East Bay) and was killed in many places by the freshets in the winter and spring of 1936. It was with eggs on June 7 on St. Vincent Bar and continued to produce eggs until autumn.

Crepidula formicata L.

St. Vincent Bar, August 1, September 26; Crooked Island Sound, November 21; St. Joe Bay, March 26.

Selia adamsii H. C. Lea

St. Vincent Bar; August 1, September 26.

Cerithium floridanum Morch

St. Vincent Bar, June 7; Platform Bar, June 6, August 20; Hile's Shallow Bed, July 11; Picolyne Bar, August 21.

Eupleura caudata sulcidentata Dall

Green Point Lump, March 16; Crooked Island Sound, November 21; Porter's Bar, April 15.

Thais floridana floridana Conrad

This oyster-destroying conch was common on St. Vincent and Hile's Deep and Shallow Bars, but was rare (Picolyne) or absent elsewhere. It was depositing egg capsules during all of June and at least until July 11.

Anachis obsea ostricicola Melv.

This little snail was often abundant among shells on the oyster bars throughout Apalachicola Bay. It persisted in salinities as low as 0.6 ‰.

Mitrella lunata Say

Picolyne Bar, August 10.

NUDIBRANCHS

Several species of nudibranchs were collected on St. Vincent Bar, Porter's Bar, and Cat Point, June 5 to September 26. Representatives of these have been deposited in the United States National Museum, but none have been identified.

TUNICATA

Molgula occidentalis Traustedt

This asidian was not uncommon during the summer on the oyster bars in the saltier area of Apalachicola Bay, but it never attained large size as in St. Joe Bay and Crooked Island Sound.

CHORDATA

PISCEA

Felichthys felis (L.)

The gaff-topsail catfish was common throughout Apalachicola Bay and in the mouth of the river. On the oyster bars small schools often gathered beside a boat while oysters were being examined, and snatched up the small animals that were thrown overboard.

Leptocephalus conger (L.)

Leptocephalid larvae were taken in tow nets in Apalachicola Bay at the following stations: (February 4-15, 1936): 11-mile Lump, Picolyne Bar, Hile's Shallow Bed, East end of Gorrie Bridge, Cat Point, St. Vincent Bar.

Bascanichthys scuticaris (Goode & Bean)

Snake eel; St. Vincent Bar; April 7, S:2.93; a specimen about 50 mm. long tonged from bottom with oysters.

Brevoortia tyrannus (Latrobe)

Young were taken in tow nets; Porter's Bar, February 14; Hagen's Flats, April 13, S:2.63; Cat Point, April 15, S:3.63; St. Vincent Bar, April 14.

Anchoziella mitchelli (Cub. & Valen.)

Young in tow net; Porter's Bar, February 14.

Syngathus floridae (Fordan & Gilbert)

Platform Bar, July 1; common in St. Joe Bay.

Mugil cephalus L.

Common in Apalachicola Bay.

Trichonotus carolinus (L.)

Pompano often leaped near the boat over the oyster bars in Apalachicola Bay during the summer.

Lagodon rhomboides (L.)

Young pinfish in tow nets; east end of Gorrie Bridge, February 6.

Leiostomus xanthurus Lacepede

Young spot in tow net; east end of Gorrie Bridge, February 6; Porter's Bar, February 14.

Micropogon undatus (L.)

Young croakers in tow net, east end of Gorrie Bridge, February 6; Porter's Bar, February 14; Cat Point, April 16. S:2.29.

Pogonias cromis (L.)

Schools of sea drum enter Apalachicola Bay and do damage on oyster beds. During June, 1935 a number were caught off the docks at the mouth of the Apalachicola River.

Microgobius thalassimis Jordan & Gilbert

Young in tow net; Porter's Bar, February 14.

Gobionellus hastatus (Girard)

Cat Point, tow net; April 15, S:2.29.

Gobiosoma boscii Lacepede

The naked goby commonly lived in old oyster shells in Apalachicola Bay and St. Joe Bay. It was observed with eggs and young July 19, April 17, St. Vincent Bar, April 13, East end of Gorrie Bridge; April 15, East Hole, Cat Point. Salinities as low as 0.05 were tolerated.

Opsanus tau (L.)

The toadfish was commonly found in oyster shells in the saltier parts (S: 4.59) of Apalachicola Bay. On May 16 one was observed guarding eggs on Paradise Flats.

Gobiosox strumosus Cope

Clingfishes were common in oyster shells in the saltier parts (S: 1.30 \pm) of Apalachicola Bay and St. Joe Bay. Individuals guarding clutches of eggs and newly hatched young on March 30 on Hile's Deep and Shallow Beds.

Hypsoblennius hentz (Lesueur)

This little blenny was common in oyster shells on the bars in Apalachicola Bay and St. Joe Bay. It did not endure low salinities as well as *Gobiosoma*.

Urophycis sp.

A young hake was caught in a tow net on Porter's Bar, February 14.

REPTILEA

Caretta caretta (L.)

Loggerhead turtles were seen at times during the summer over the oyster bars in Apalachicola Bay.

Malaclemys macrospilota (W. P. Hay)

Diamond-back turtles live in the salt marshes near Indian Pass and there are associated with oysters on shallow, or "Coon," bars.

AVEA

Various birds frequented Apalachicola Bay. In summer the commoner species were pelican, cormorant, common tern, least tern, royal tern, Caspian tern, and laughing gull. In winter there were many herring gulls and broad-bill ducks. At times cuban plovers, skimmers, oyster catchers, and other shore birds were common. In the bayous tributary to the bay were herons.

MAMMALEA

Tursiops truncatus (Montague)

Schools of porpoises were seen almost daily, feeding along the oyster bars in Apalachicola Bay and at Indian Pass.

In St. Joe Bay, only ten miles from Apalachicola Bay, and in Crooked Island Sound, 35 miles away (where fresh water never enters in large quantities, large flats of eel grass exist, and there is a considerable body of deep water), the fauna is quite different. Animals and plants are common which have not been seen in, and are probably absent from, Apalachicola Bay. Among these may be mentioned:

Algae: *Acetabularia crenulata* Lebour, *Dasycladus clavaeformis* (Roth.) Ag., *Batophora oerstedii* Ag.

Eelgrass: *Zostera marina* L.

Polycladidida: *Discocelis grisea* Pearse, *Stylochoplana floridana* Pearse, *Conjugouterus parvus* Pearse, *Leptoplana variabilis* Girard, *Thysanozoon brocchii* Grube, *Pseudoceros maculosus* Pearse, *Oligogoclado floridanus* Pearse.

Bryozoa: *Bugula neretins* L.

Echinodermata: *Astropecten articularis* (Say), *Lucidia clathrata* (Say), *Echinaster spinulosus* Verrill, *Ophiothrix angulata poecila* H. L. Clark, *Ophioderma brevispinum* (Say), *Lytechinus variegatus carolinus* (A. Agassiz), *Mellita quinquiesperforata* (Leske), *Moiria atrops* Lamarck, *Plagiobrissus grandis* (Gmelin), *Leptosynapta multigranulata* H. L. Clark.

Crustaceae: *Peltogaster* sp. on *Pagurus*; *Leucothoe spinicarpa* (Albidg.) in *Molgula* and *Styela*: *Melita fresneldii* (And.), *Elasmopus posillimanus* Bate, *Polychaera antarctica* (Stebbing), *Paracerceis caudata* (Say in *Didemnum* and *Styela*, *Ligyda exotica* (Roux), *Peneus braziliensis* Latreille, *Trachypeneus constrictus* Stimpson, *Eusicyonia laevigata* (Stimpson), *Tozeuma carolinensis* Kingsley, *Crangon packardii* Kingsley, *Conchedytes domestica* (Gibbes), *Pagurus longicarpus* Say, *P. bonairensis* Schmitt, *Portunus spinimanus* Latreille, *Panopeus americanus* Saussure, *Neopanope texana sayi* (Smith) in *Styela*, *Pinnixa cylindrica* (Say) in *Pecten*, *Sesarma cinera* Say, *Uca minax* (Le Conte), *Pelia mutica* (Gibbes) in *Molgula*, *Podochela riisei* Stimpson.

Arachnidea: *Limulus polyphemus* (L.) breeding March 26, 1936.

Insecta: a caddis-fly larva in a spun tube.

Pelecypods: *Pecten gibbus* (L.), *Modiolaria lateralis* Say, *Cardita floridana* Conrad, *Teredo bartschi* Clapp.

Gastropodea: *Calliostoma j. jujubinum* Gmelin, *Cerethium muscarum* Say, *Murex rufus sallianus* A. Adams, *Thais undata* Lamarck, *Tritonalia cellulosa* Conrad, *Nassa vibex* Say, *Busycon p. perversum* L., *Fasciolaria distans* Lamarck, *Tethys protea* Rang, *Cavolina longirostris* Blainville, *Urosalpinx perrugatus* Conrad, *Conus pealii* Green, *Murex rufus* Lamarck, *Turbo castaneus* Gmelin.

Cephalopodea: *Octopus vulgaris* Lamarck.

Enteropneusta: *Dolichoglossus kowalevski* (A. Agassiz).

Tunicates: *Amaroucium bermudae* Van Name, *Didemnum candidum* Savigny, *Styela plicata* Lesueur, *Molgula occidentalis* Traustedt, *Distaplia bermudensis* Van Name, *Diplosoma macdonaldi* Herdman *Trididemnum* sp.

Fishes: *Hippocampus zosterae* Jordan & Gilbert, *Chilomycterus schaeppi* (Walbaum).

When in the first week in January 1935 freshets in Georgia caused the Apalachicola River to discharge fresh water into Apalachicola Bay, many animals which had survived the low temperatures disappeared. *Petrolisthes*

armatus (Gibbes) had been abundant but was gone completely by the end of January. On the other hand *Carinogammarus mucronatus* (Say) appeared first in East Bay on February 6 and by April 15 had spread over the whole of the east end of Apalachicola Bay (Porter's Bar, Platform Bar, East Hole). Many oysters and barnacles died; the former largely where water previously had been fairly saline (St. Vincent Bar), the latter where water had been fairly fresh (East Bay). Among the types which tolerated fresh water best the following may be mentioned: *Eurypanopeus*, *Nereis*, *Carinogammarus*, *Gobiosoma*, *Gobiosox*, *Balanus*, *Ostrea*, and *Eustylochus*.

RELATIONS OF OYSTERS TO ANIMALS ASSOCIATED WITH THEM—Certain of the animals which live on oyster beds unquestionably injure oysters. Among these are boring sponges; oyster "leeches"; polychaete worms; carnivorous gastropods, or conchs; boring clams; certain crabs; and fishes such as the drum. Others are not injurious to oysters; they are commensals or more or less without definite relations. Some animals do not attack oysters directly but injure them by competing for space to live and food—sponges, barnacles, mussels, ascidians, etc. Any change in environment may upset the established balance in a society and perhaps cause one type to decrease and another to increase. A certain societal complex goes with oyster "leeches." Along the coast of Florida from Apalachicola Bay to Indian River *Stylochus inimicus* is often common and the little oyster crab, *Pinnotheres ostreum*, is rare or absent. On the east coast north of Indian River the oyster crab is common. This animal probably does an oyster in which it lives little or no injury. The writers have had their attention fixed on polyclad worms in relation to oysters, but have incidentally noticed that in certain areas in Apalachicola Bay (St. Vincent Bar, Hile's Shallow Bed) conchs, chiefly *Thais f. floridana* Conrad, often kill oysters, but on other oyster beds (Porter's Bar, East Hole), where "leeches" are fairly common, these molluscs are rare or absent. All oyster pests do not flourish under the same conditions. Each species has its own peculiar environmental complex in which it is at its best. The little porcellanid crab, *Petrolisthes armatus* (Gibbes), probably does no harm to oysters, though it is often abundant on the bars in Apalachicola Bay. It appears to flourish under about the same condition as the oyster "leech," *Stylochus inimicus*, and, as it is more easily discovered, may be used as an indicator of conditions favorable for "leeches."

CONTROL OF OYSTER "LEECHES"

Perhaps the best way to kill *Stylochus* is to inundate oyster beds with fresh water. After the freshets in the winter and spring of 1936 not an oyster "leech" could be found in Apalachicola Bay. Perhaps in the future it may be possible and financially expedient to control oyster "leeches." There is little hope of exterminating the worms by chemicals, as they tolerate rather high concentrations of injurious substances. Expense would make

such measures inexpedient and oysters as well as pests would perhaps be killed.

Attempts were made to feed *Stylochi* to fishes kept in dishes in the laboratory. In this way four fishes which commonly occurred on oyster bars were tested; toadfish, sea robin, a goby (*Gobiosoma boscii*), and a blenny (*Hypsoblennius hentz*). Only the blenny ate *Stylochi*. One fish ate 4.5 large worms in four days.

INJURY TO OYSTERS BY "LEECHES"

There is no question that *Stylochus inimicus* enters, devours, and destroys oysters. The oyster fights the worm, as has been described (p. 632). The worm is present in living oysters continually (Fig. 37). Certain persons who visited Porter's Bar in Apalachicola in 1932-1933 when the oysters were dying rapidly maintain that *Stylochus* was solely responsible for the extermination of oysters; others who worked on the bar at that time say that many oysters died before they were attacked by "leeches," and that *Stylochus* was only a contributing cause of mortality. On all the oyster beds in Apalachicola Bay polychaete worms are continually making holes about the margins of the shells of living oysters; sporozoans are present in the bodies of oysters; conchs devour many oysters in certain areas; boring clams and sponges make holes in oyster shells; floods of fresh water may kill off considerable number of oysters; low temperature and high winds at times do great injury. There are so many things present in the bay at all times which may kill oysters that it is difficult to say that one of them is wholly responsible. Our observations make it appear that *Eustylochus* does not attack living oysters, but preys on barnacles and at times enters and eats oysters that are sick or dying.

It has been suggested that the cleaning of grounds and the careful planting of vigorous stock of carefully culled oysters would eliminate the oyster leech pest. There is unquestionably much to be done in Apalachicola Bay, and on the whole Florida coast where *Stylochus* occurs, for the improvement of methods of oystering. Careful preparation of beds, planting, and harvesting would doubtless result in better oysters and increased production, but would not eliminate *Stylochus*. Each worm may lay 20,000 eggs, which can hatch into swimming larvae that are carried everywhere by tidal currents. A "leech" may grow from egg to maturity in a couple of months. It is therefore possible for the most carefully prepared bed to become infested in a season when salinities and temperatures are high.

DISCUSSION

PREDATOR OR PARASITE—There is some question in the minds of many students of polyclads as to whether *Stylochus inimicus* Palombi should be called a parasite or not. Palombi (1931) argues that it is merely a commen-

sal. Roughley (1935) states that *Leptoplana australis* (Schmarda), which feeds on oysters in the Australian region, does not kill oysters but enters dead or dying individuals. He looks upon the worm as a scavenger. None could be induced to enter normal oysters in auaria. Bock (1925) affirms that *Stylochus ferox* Bock destroys young oysters along the coast of Japan. He looks upon the worm as a predator. On the coast of Florida there is no doubt that *Stylochus inimicus* enters living oysters, gradually devours their soft parts, and finally kills them.

Small animals which have intimate relations with larger animals, called hosts, are usually classified by zoologists under three groups: (1) Commensals live in or on their hosts without benefitting them. They may obtain food, shelter, or other benefits from their hosts or they may merely use the host as they would any other similar object. The crustaceans that live in the tubes or annelid worms and the little crabs that commonly dwell in oysters are examples of commensals. (2) Symbionts live with hosts which they benefit, and in return receive something from their hosts. A bird which sits on the back of a cow and picks off insects or ticks thus obtains food and frees its hosts of injurious parasites. (3) Parasites injure their hosts, and usually do so without causing death. A hookworm may cause anemia in its host. It often shows a tendency to attack only one species or one group of hosts; it is adapted to the temperatures, chemical characteristics, and other peculiarities of the host. A mosquito feeds only on homeothermic animals and will at times attempt to insert its proboscis into almost any warm object. A beef tapeworm will not live in any definite host except man, not even in anthropoid apes, and requires cattle for its secondary host; it has lost its enteron completely and must live within a host during all active stages in its life cycle. Yet a beef tapeworm rarely is even a contributing cause of the death of its host. Hosts generally have some degree of tolerance for their parasites (Herms 1932) and parasites, while they injure their hosts, seldom completely eliminate the sources of their benefits. This is adaptation.

Stylochus inimicus does not differ anatomically from nearly related free-swimming predaceous polyclads. It shows some adaptation to oysters in that it seldom feeds on anything else. On the other hand, oysters attempt to prevent the worms from entering and often enclose them within shell substances when they do enter. The worms if successful in their attack gradually devour and kill the oysters. *Stylochus* is properly to be looked upon as a predaceous animal which may in time become a parasite of oysters but has not as yet become adapted enough to be called one.

STRENGTH AND WEAKNESS OF *STYLOCHUS*—On the whole *Stylochus inimicus* is a hardy animal. In common with many other marine animals it can tolerate low oxygen (p. 620), withstand poisonous substances in rather high concentrations (p. 623), and endure prolonged starvation (p. 617). Its weaknesses are inability to remain active and alive (a) at low temperatures and (b) in low salinities. In its tolerance of such extremes it is less hardy

than its associate on oyster beds, *Eustylochus meridionalis*. Oysters are sensitive to temperature changes (Hopkins 1931). They tend to open when temperatures rise and close when there is a decrease. Above 20°C. they may feed about 20 hours daily, but do not feed at all below 4°C. (Nelson 1928). Galtsoff (1928) shows that feeding of oysters does not take place below 5°C. and often stops at 6-7°C. Spawning begins at about 20°C. (Nelson 1928). *Stylochus* is active between 12°C. and 34°C. It therefore cannot migrate far north on the Atlantic Coast. Up to the present it has been reported only along the Florida coast from Pensacola Bay on the west to Indian River on the east. It cannot tolerate salinities below 6 0/00 and does not lay eggs when they are below about 15 0/00. At summer temperature eggs require about eleven days for the development of a pelagic, swimming larva. These facts indicate that the most promising lines of attack and perhaps ultimate control of the pest will be through the use of low temperatures and freshwater.

CAUSES OF MORTALITY OF OYSTERS—In Apalachicola Bay oysters are decreasing in size and numbers. As long as 1893-1895 Swift (1897) recorded similar trouble and mentioned over-fishing, freshets, freezes, and hurricanes as contributing causes. The same obstacles to successful oystering obtain today. In addition to over-exploitation by man and decimation by extreme variations in environment, there are many living organisms that help to depopulate oyster beds. Some of these compete with oysters for space and food—algae, barnacles, mussels, sponges. There are enemies which continually attack oysters—bacteria, ciliates (Orton 1924), boring sponges, starfishes, boring clams, predaceous gastropods, crabs, fishes, birds and mammals. Not all of these are of apparent significance on the Florida coast. Oyster larvae are known to be eaten by ctenophores, worms, barnacles, copepods, mussels, clams, adult oysters, and tunicates (Nelson 1915, 1921). There are internal parasites which live within the soft bodies of oysters—spirochaetes, sporozoans, trematodes. There are many animals continually or intermittently present on oyster beds. When man has not collected oysters these tend to keep the population within the usual limits. When there has been over-fishing and destruction by culling, tonging, or dredging, these may more easily destroy weakened oysters and cause such mortality that bars become commercially unproductive. Polyclads, particularly the species known as the oyster "leech," in Florida are perhaps never the sole cause of heavy mortality on Florida oyster beds. They flourish and increase when there has been a prolonged drought and the water on the oyster beds becomes salty enough (S:15) to permit them to reproduce. When they attack oysters they may be assisted by other organisms or physical factors which weaken, open, or kill oysters and thus render them easy to attack. High mortality on an oyster bed is probably never due to one single cause, but to a number of contributing unfavorable circumstances. This statement is not an attempt to whitewash the oyster "leech." The soft, flat, sneaking, slippery, hungry little

worm is a dark villain on oyster bars, and at times when circumstances make a favorable season does much damage.

SUMMARY

1. *Stylochus inimicus* Palombi has for many years been an enemy of oysters along the coast of Florida and at times abundant enough to constitute a serious pest.

2. *Stylochus* is a polyclad worm but is commonly known as the oyster "leech" in Florida.

3. The anatomy is described.

4. A single *Stylochus* may lay as many as 21970 eggs in less than a month. At summer temperatures ($28^{\circ}\text{C.} \pm$) these develop into a pelagic, ciliated larva in about eleven days. *Stylochi* usually brood their clutches of eggs until they hatch.

5. *Stylochus* grows rapidly and probably becomes sexually mature in less than two months under favorable conditions. It probably may live for as long as a year.

6. *Stylochus* does not crawl about when temperatures are below 12°C. and above 34°C. It crawls at a rate of about 40 mm. per second at 25°C. *Stylochus* dies below 0°C. and at 42°C. *Eustylochus*, a species also found on oyster beds, lives for hours at -2°C. and dies quickly at 39°C.

7. Eggs increase in diameter when placed in hypo- and hyper-tonic salt solutions because of the unusual osmotic pressure, caused in the first case by the low concentration of the dissolved salts in the surrounding medium and in the second case because of the low activity coefficients of the dissolved salts in higher concentrations.

8. *Stylochus* can live for days in very low concentrations of dissolved oxygen. At 26.5°C. an individual uses about 0.1 cc. of oxygen per gram of body weight per hour. When *Stylochi* were kept in closed containers progressively less oxygen was used each day, but all the oxygen present was not used up while animals were alive.

9. Exposed in dry dishes to air of 72-77% humidity *Stylochi* lived eight hours in open dishes and fifteen hours in covered dishes at 25.2 to 26.5°C. They lived several days in pails of shells without water. *Stylochi* recovered after losing 55% of body weight by desiccation.

10. *Stylochus* can live in salinities as low as 6 0/00, but does not lay eggs in concentrations below 15 0/00. *Eustylochus* tolerates lower salinities (0.6 0/00) than *Stylochus*. Larvae are less able to tolerate low salinities than adults.

11. The toleration of *Stylochus* for various dilutions of solutions of 25 different chemicals in sea water was studied. None of the substances gave promise as an agent for control measures.

12. *Stylochus* feeds largely on oysters. It will also eat barnacles and certain snails but refuses fish, shrimp, and most species of snails. It will enter and devour living oysters.

13. In Apalachicola Bay *Stylochus* was generally most abundant where oysters grew in water of relatively high salinity. Data for fifteen stations where monthly observations were made for a year are presented.

14. *Stylochus* will creep into a living oyster, which usually tries to shut off the intruder by building a partition. Sometimes worms are thus covered over and buried in the shell.

15. Many species of plants and animals are associated with oysters on the beds in Apalachicola Bay. A list of those identified is given.

16. *Stylochus inimicus* is a predator, not a parasite, on oysters.

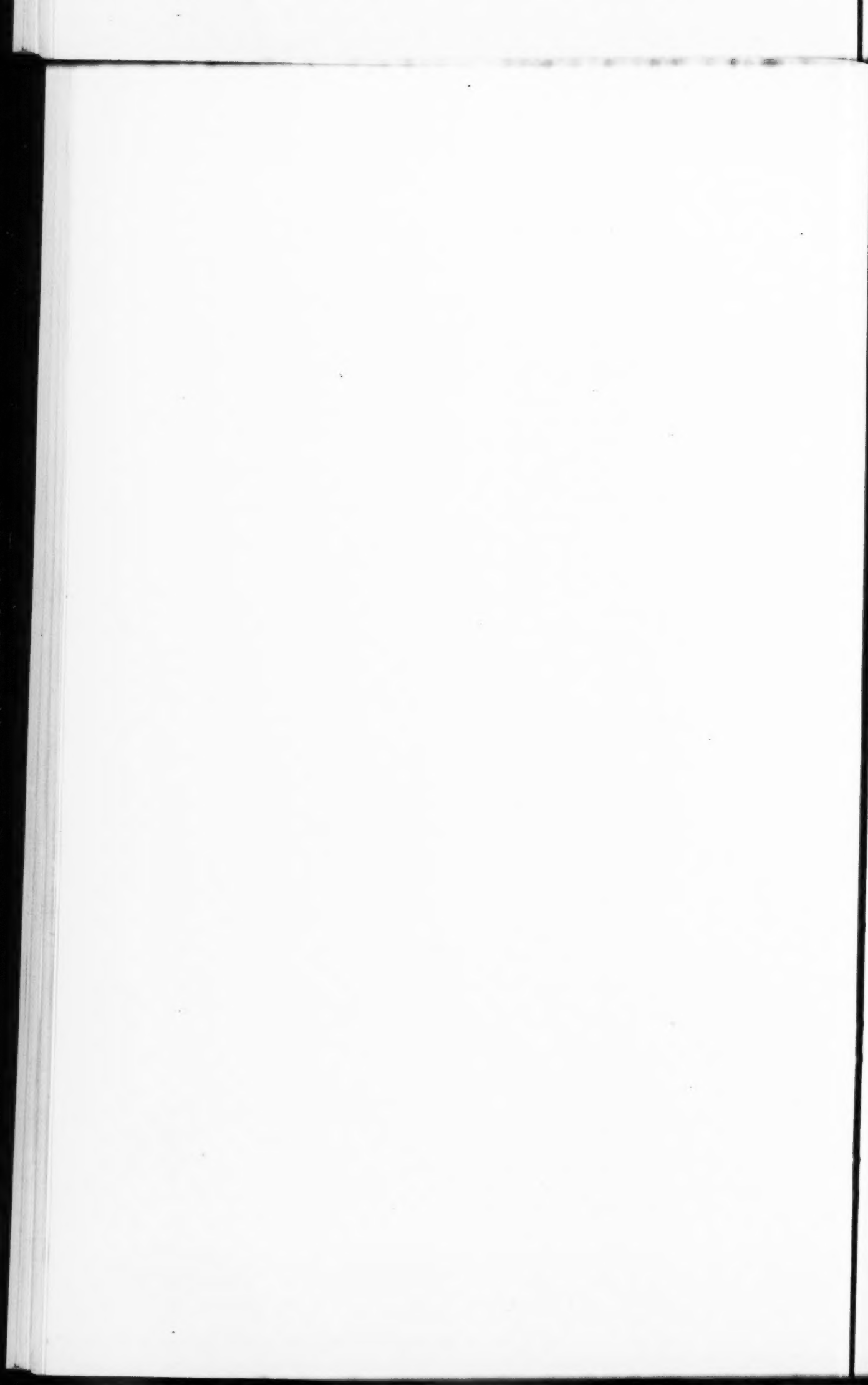
17. *Stylochus* tolerates poisonous chemicals and low oxygen concentrations, but is susceptible to low temperatures and fresh water. Control measures should perhaps take cognizance of these facts.

18. When oysters die in numbers on beds probably several factors contribute to cause the mortality. The oyster "leech" may kill oysters but probably rarely, if ever, is the sole "cause" of the extermination of oysters in a particular locality.

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